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AMERICAN MALACOLOGICAL BULLETIN

VOLUME 4 NUMBER 1 FEBRUARY 1986

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Cover. The eolid nudibranch *Cerberilla mosslandica* McDonald & Nybakken. A special symposium on nudibranchs is one of three symposia planned for AMU 1986 in Monterey, California. See announcement in this issue.

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February 1986

MIDDLE TERTIARY ROCKY SUBSTRATE MOLLUSKS FROM BAJA CALIFORNIA SUR, MEXICO

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ABSTRACT

Middle Miocene rocky substrate mollusks occur in living positions or very near their original habitat in two areas of northwestern Baja California Sur, Mexico. Calyptraeids, *Tegula, Siphonaria, Vermetus,* and others that are barely distinguishable in shell morphology from their Holocene relatives are associated with wide-ranging Tertiary Caribbean index species of *Turritella.* Radiometrically dated basalt flows overlying the marine fossiliferous sediments provide youngest age estimates of 14.5 m.y. and 9.7 m.y. for molluscan assemblages that precisely define middle Miocene shorelines. Paleontologic and potassium-argon data can be applied to phylogenetic studies as well as paleogeographic reconstructions of the tropical eastern Pacific and the Baja California peninsula.

Unattached rocky substrate faunules of the littoral zone are uncommon in the fossil record and extremely rare in pre-Pleistocene sediments associated with radiometrically dated volcanic rocks. Mollusks representing rocky habitats occur in Baja California Sur, Mexico in outcrops of the Isidro and San Ignacio Formations, each of which is overlain by middle Miocene basalt flows. Barely distinguishable morphologically from Holocene taxa, most of the taxa indicate specific environments rather than a refined age. Many cap-shaped "limpets" noted in the field were identified as calyptraeids after preparation of the apertures. Co-occurring turritellids with wide-spread Tertiary Caribbean distributions permit correlation of isolated near-shore deposits near the towns of La Purisima and San Ignacio with deeper neritic sedimentary deposits elsewhere in Baja California, Panama, Costa Rica, the Dominican Republic, Colombia, and Peru.

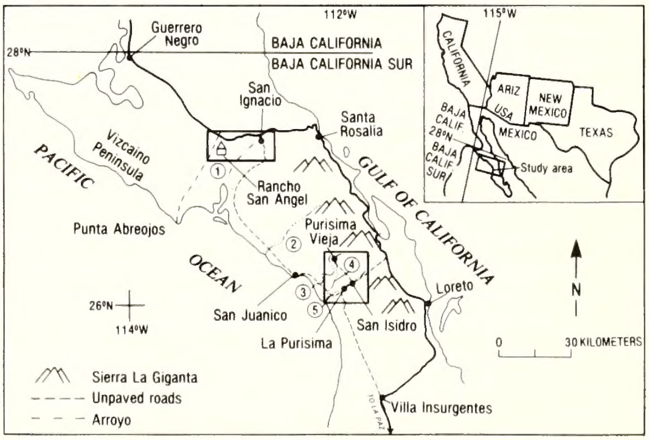
112°W
115°W
Guerrero Negro
28°N
BAJA CALIFORNIA
BAJA CALIFORNIA SUR
San Ignacio
Santa Rosalia
Vizcaino Peninsula
PACIFIC
OCEAN
GULF OF CALIFORNIA
Rancho San Angel
Punta Abreojos
Purisima Vieja
San Juanico
San Isidro
La Purisima
Loreto
Villa Insurgentes
TO LA PAZ
26°N
114°W
1
2
3
4
5
N
0
30 KILOMETERS
Sierra La Giganta
Unpaved roads
Arroyo
CALIFORNIA
ARIZ
NEW MEXICO
USA
TEXAS
MEXICO
BAJA CALIF.
28°N
BAJA CALIF SUR
Study area

Fig. 1. Study areas in northwestern Baja California Sur, Mexico. Numbers refer to arroyos mentioned in text: 1 Arroyo San Ignacio, 2 Arroyo San Raymundo, 3 Arroyo Mezquital, 4 Arroyo San Gregorio, 5 Arroyo La Purisima.

GEOGRAPHIC AND GEOLOGIC SETTING

Two areas in Baja California Sur yielded abundant rocky substrate intertidal to sublittoral mollusks: Purisima Vieja, a palm grove about 25 km northwest of San Isidro in Arroyo San Gregorio, and Arroyo San Ignacio, downstream from the town of the same name (Fig. 1). About 160 km apart, the two localities are far up canyons that drain westward to the Pacific Ocean from the crest of the Sierra la Giganta. Fossiliferous outcrops are exposed only in canyon walls, intervening areas being covered by younger basalt flows, volcanically-derived conglomerate, and terrace deposits.

Marine sediments with rocky substrate mollusks are mapped as the Isidro Formation in the La Purisima area and as the San Ignacio Formation in the north (Mina, 1957; McLean and Hausback, 1984). Both formations have numerous lithic facies changes, horizontally gradational rock types that vary from limy marls and coquina through fine grained siltstones and sandstones to coarse pebbly sands and beach deposits. Rocky substrate faunules are represented mainly in isolated outcrops near the upper parts of these formations where they grade into nonmarine sandstone or are covered by basalt flows.

Mina (1957) showed the San Ignacio Formation extending as far south as Arroyo San Raymundo, several canyons north of the La Purisima area. Some reports (Hertlein and Jordan, 1927; Beal, 1948) used "Ysidro," an alternate spelling of "Isidro," for the strata in both study areas. Reconnaissance mapping up the canyons between Arroyo la Purisima and Arroyo San Ignacio (McLean, Hausback and Knappe, 1984), together with paleontologic and radiometric studies in progress should provide data for determining whether the two formations can be mapped as a single unit. Present evidence indicates that the Isidro Formation ranges in age from earliest early Miocene to late middle Miocene, or, younger than 23 m.y. to older than 14.5 m.y., the radiometric ages of underlying and overlying basalt flows reported by Hausback (1984). The base of the San Ignacio Formation is unknown but a basalt cap of 9.7 m.y. (Sawlan and Smith, 1984) provides a youngest estimate of late middle Miocene for the uppermost sediments. Mollusks from the two formations are different, those of the Isidro Formation having stronger Tertiary Caribbean affinities and those from the San Ignacio Formation including more endemic taxa, some Tertiary Caribbean species, and a number of mollusks similar to those reported by Olsson (1932) from the Tertiary of Peru.

FIELD WORK AND SOURCES OF SPECIMENS

Most of the mollusks reported on here were collected in March, 1984 by the author and by Thomas M. Cronin, U.S. Geological Survey, Reston, Virginia, who sampled the same outcrops for ostracods. The fossils were collected from sediments overlain by volcanic flows that had previously been dated radiometrically by James G. Smith (Sawlan and Smith, 1984) and Brian P. Hausback (1984). Field work was supported by the Consejo de Recursos Minerales de Mexico and the U.S. Geological Survey as part of a joint program to study the geological history of the Baja California peninsula and the Gulf of California. Comparative specimens were examined from the samples of McLean and Hausback (locality 383-11-2) and the collections of Stanford University, the California Academy of Sciences, and the University of California, Berkeley.

MODE OF PRESERVATION AND PREPARATION

Gastropods and pelecypods from the upper part of the Isidro Formation at Purisima Vieja retain original shell material but require careful soaking in an industrial detergent ($C_{24}H_{47}N_2O_2Cl$) or excavation with vibra tools to remove the calcareous sandy matrix. Preserved in living positions, the capped-shaped "limpets" proved on preparation to be mainly calyptraeids, the horse hoof limpet *Hipponix*, and several unidentifiable forms. No patellacean limpets were found in this area during the 1984 field season, although several recrystallized specimens were collected previously from Arroyo Mezquital (McLean and Hausback locality 383-19-7). These individuals may be stratigraphically lower in the Isidro Formation, where they are associated with fragments of *Turritella bifastigata* Nelson, *Trochita spirata* (Forbes), *Trochita trochiformis* (Born), *Anadara (Esmerarca)* sp., and *Cardita (Cardites)* sp. of Smith (1984).

Specimens from the San Ignacio Formation differ considerably in preservation; better material was found in limy sandstones, crumbly specimens in softer, finer grained beds. Preservation varied within outcrops, and careful collecting was commonly rewarded by naturally prepared specimens that retained even fine shell sculpture.

FOSSILS FROM PURISIMA VIEJA

Rocky substrate mollusks of the littoral zone occur in living position on a low bench on the east side of Arroyo San Gregorio about ½ km upstream from the palm grove at Purisima Vieja (84JS16, Fig. 2). A coarse pebbly sandstone ledge about a meter above the stream bed provided a hard substrate for abundant specimens of *Crepidula, Crucibulum, Tegula, Protothaca,* and small *Anadara*; the most important taxon is *Siphonaria maura pica* (Sowerby, 1835), an air-breathing species that is a reliable indicator of a shoreline. Directly across the arroyo to the west the calyptraeids occur at stream level, overlain by several meters of marine fossiliferous sandstone and tuffaceous material (84JS17, Fig. 2). Randomly oriented fossils include large *Melongena* sp. cf. *M. melongena* (Linnaeus, 1758), *Turritella* sp. cf. *T. crocus* Cooke, 1919, and fragments of *Vermetus* sp. cf. *V. contortus* (Carpenter, 1857), coral, and undetermined razor clams. At the same stratigraphic level a few hundred meters downstream (McLean and Hausback locality 383-11-2) occur specimens of *Turritella altilira* Conrad, 1857, *Cerithium* ? sp. and *Chione* sp.

Reconnaissance mapping by McLean and Hausback (1984) shows that the upper part of the Isidro Formation, which contains the rocky substrate assemblage, grades upward into nonmarine sandstone and conglomerate of the Comondu Formation, the lower part of which contains an interbedded basalt flow (McLean and Hausback locality 383-11-1). This basalt has a radiometric age of 14.5 m.y. (Hausback, 1984) which indicates that the *in situ* fossils and shoreline are middle Miocene in age.

Because neither color nor soft parts are preserved, the calyptraeids, *Siphonaria, Vermetus,* and *Hipponix* are indistinguishable from taxa living today in the tropical eastern Pacific. The large *Melongena* (Pl. 1, Figs. 4, 8) is probably the same species as *Melongena melongena* (Linnaeus, 1758) living in the West Indies; it is useful for melongenid phylogeny, since an older taxon, *Melongena melongena consors* (Sowerby, 1850), was reported (Smith, 1984) from the lower part of the Isidro Formation farther downstream in Arroyo San Gregorio (McLean and Hausback locality 383-18-2).

Because outcrops of the Isidro Formation are restricted to canyon walls and mapping has been of a reconnaisance nature, precise correlations between outcrops have not yet been made. Specimens from Purisima Vieja of *Turritella* sp. cf. *T. crocus* Cooke, 1919 may be the same species as the common *Turritella* from a locality 15-20 km downstream in San Gregorio (CAS locality 54066). It is one of half a dozen species of *Turritella* found in the Isidro Formation, and one whose distribution could reflect ecologic as well as age differences within the formation.

Previous work on the mollusks of the Isidro Formation concentrated on the abundant fauna of the lower, older part

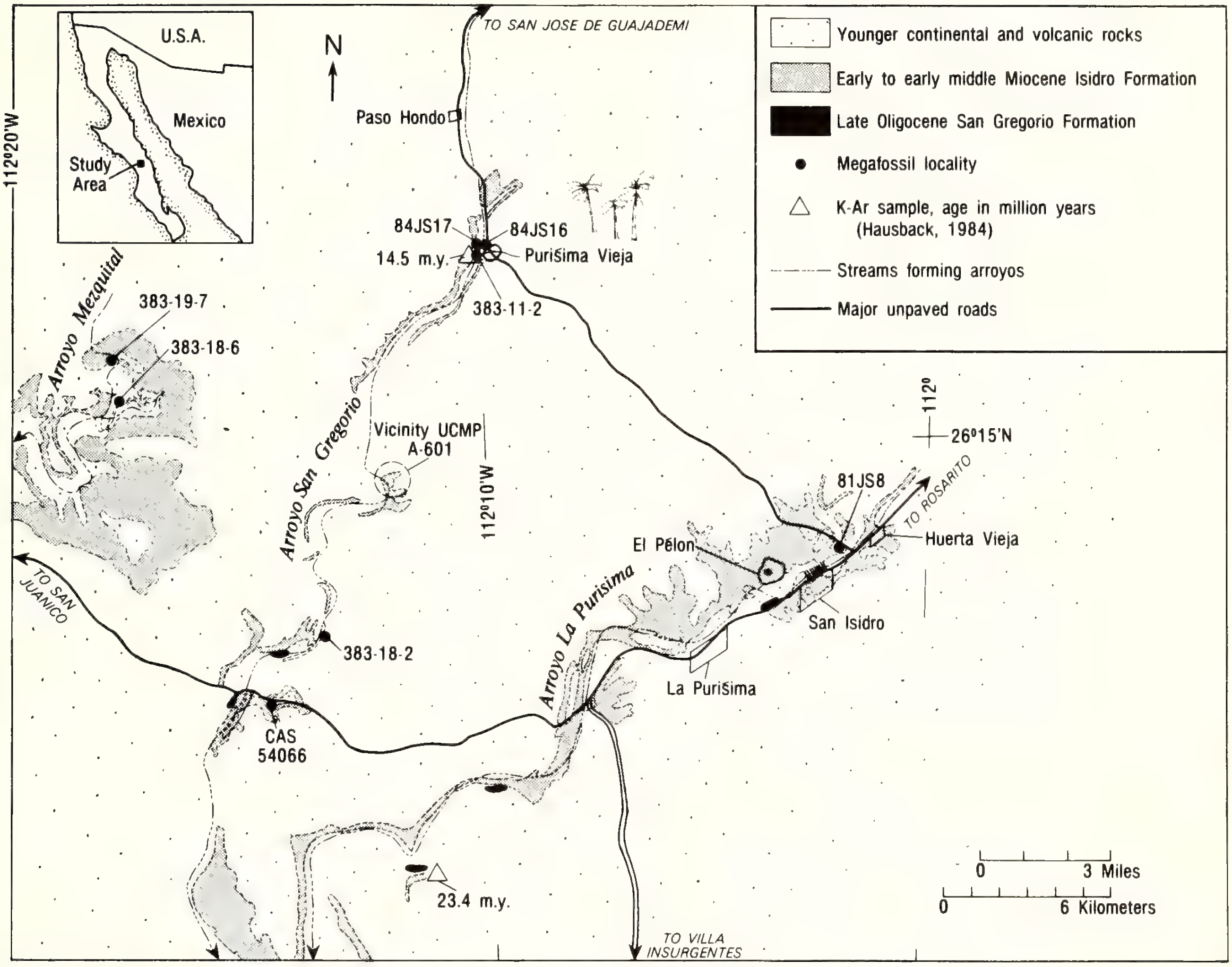
U.S.A.
Mexico
Study Area
112°20'W
N
TO SAN JOSE DE GUAJADEMI
Younger continental and volcanic rocks
Early to early middle Miocene Isidro Formation
Late Oligocene San Gregorio Formation
Megafossil locality
K-Ar sample, age in million years (Hausback, 1984)
Streams forming arroyos
Major unpaved roads
Paso Hondo
84JS17
84JS16
14.5 m.y.
Purisima Vieja
383-11-2
Arroyo Mezquital
383-19-7
383-18-6
Arroyo San Gregorio
Vicinity UCMP A-601
112°10'W
112°
26°15'N
81JS8
TO ROSARITO
Huerta Vieja
El Pelon
Arroyo La Purisima
San Isidro
La Purisima
TO SAN JUANICO
383-18-2
CAS 54066
23.4 m.y.
0 3 Miles
0 6 Kilometers
TO VILLA INSURGENTES

Fig. 2. Purisima Vieja and surrounding area, Baja California Sur, Mexico. Geology after McLean and Hausback (1984).

of the formation (e.g., 81JTS8), especially near the type locality at the town of San Isidro in Arroyo La Purisima (Hertlein, 1925; Hertlein and Jordan, 1927; Smith, 1984). Species listed by Beal (1948) that were collected by W.S.W. Kew from the area between Pozo [Paso] Hondo and Purisima Vieja (USGS locality 9157) seem, from inspection of the matrix, to have been collected from down section and downstream from the palm grove rather than upstream in the direction of the younger, nonmarine rocks included in the basal Comondu Formation. Specimens of *Turritella* sp. cf. *T. inezana bicarina* Loel and Corey, 1932 collected by W.L. Watts (locality UCMP A-601) and illustrated by Merriam (1941) and Loel and Corey (1932) also came from this downstream section.

Molluscan species from the upper part of the Isidro Formation at Purisima Vieja are listed in Table 1, and representative species are illustrated in plate 1.

FOSSILS FROM ARROYO SAN IGNACIO

Southwest of the town of San Ignacio an arroyo of the same name winds southwest to the head of San Ignacio Lagoon. Canyon walls are formed of white, fossiliferous calcareous sandstones and siltstones of the San Ignacio Formation, which is 60-100m thick (Mina, 1957), but obscured in places by talus slopes of volcanic boulders and by terrace deposits (Fig. 3). Throughout much of this area the San Ignacio Formation is disconformably overlain by a distinctive basalt cap referred to informally as the basalt of Rancho Esperanza (Sawlan and Smith, 1984). Originally described by Mina (1957), the San Ignacio Formation is known mainly from the molluscan fauna collected in 1921 by Marland Oil Company geologist B.F. Hake and described by Hertlein and Jordan (1927). Outcrops extend from the north side of Mexican Highway 1 near the turnoff to the town of San Ignacio to 5-10 km west of Rancho San Angel and at least 8 km down the arroyo, where an important Miocene shark fauna was found (S.P. Applegate, 1984, oral communication). Mina (1957) mapped outliers of the San Ignacio Formation as far south as Arroyo San Raymundo.

An upper limit on the age of the San Ignacio Formation fossils is provided by K-Ar ages of 9.72 and 10.1 m.y. on the

Table 1. Molluscan species from littoral, rocky substrates and associated taxa from soft sediments, northwestern Baja California Sur, Mexico.

TAXA	Purisima Vieja Isidro Formation early middle Miocene	Arroyo San Ignacio San Ignacio Formation late middle Miocene	Habitat if known from observation
GASTROPODS			
Calliostoma hannibali Hertlein & Jordan, 1927	---	x	
Calyptraea sp.	x	---	rocky substrate
Cerithium ? sp.	x	---	
Crassilabrum wittichi (Hertlein and Jordan, 1927)	---	x	
Crassispira starri Hertlein and Jordan, 1927	---	x	
Crepidula sp.	---	x	rocky substrate
Crucibulum inerme Nelson, 1870	---	x	rocky substrate
Crucibulum sp. cf. *C. scutellatum* (Wood, 1828)	---	x	rocky substrate
Cymia heimi Hertlein and Jordan, 1927	---	x	
Cypraea amandusi Hertlein and Jordan, 1927	---	x	
Drillia (Clathrodrillia) sp.	---	x	
Hipponix pilosus (Deshayes, 1832)	x	---	rocky substrate
Knefastia sp.	---	x	
Macron hartmanni Hertlein & Jordan, 1927	---	x	
Melongena sp. cf. *M. melongena* (Linnaeus, 1758)	x	---	bays, mud
Nassarius sp. cf. *N. versicolor* (C.B. Adams, 1852)	---	x	
Nerita sp. cf. *N. funiculata* Menke, 1852	---	x	rocky intertidal
Neverita (Glossaulax) sp. cf. *N. (G.) andersoni* (Clark, 1918)	---	x	
Siphocypraea sp. cf. *S. henekeni* (Sowerby, 1850)	x	---	
Siphonaria maura pica Sowerby, 1835	x	---	rocky intertidal
Solenosteira sp.	---	x	
Strombina sp.	---	x	
Tegula sp.	x	---	rocky intertidal
Terebra burckhardti Hertlein & Jordan, 1927	---	x	
Theodoxus sp. [*Neritina* of authors]	x	---	estuarine
Trochita sp. cf. *T. radians* Lamarck of Arnold and Anderson (1907)	x	---	
Trochita spirata (Forbes, 1872)	x	---	
Trochita trochiformis (Born, 1778)	x	---	
Turritella altilira Conrad, 1857	x	---	
Turritella bosei Hertlein & Jordan, 1927	---	x	
Turritella costaricensis Olsson, 1922	---	x	
Turritella sp. cf. *T. crocus* Cooke, 1919	x	---	
Turritella n. sp.?	---	x	
Vermetus sp. cf. *V. contortus* (Carpenter, 1857)	x	---	rocky intertidal
PELECYPODS			
Amiantis sp.	---	x	
Anadara sp. cf. *A. (Cunearca) nux* (Sowerby, 1857)	x	---	littoral, under rocks
Chione (Chione) richthofeni Hertlein & Jordan, 1927	---	x	
Chione (Chionopsis) sp.	---	x	
Chione sp.	x	---	
Choromytilus sp. cf. *C. palliopunctatus* (Carpenter, 1857)	---	x	intertidal
Cyclinella sp.	---	x	
Divalinga sp. cf. *D. comis* (Olsson, 1964)	---	x	
Lucina (Lucinisca) sp.	---	x	
Mytilus sp. cf. *M. canoasensis vidali* Ferreira and Cunha of Woodring, 1973	---	x	intertidal
Ostraea sp. a	---	x	rocky substrate
Ostraea sp. b	x	---	rocky substrate
Plicatula sp. cf. *P. inezana* Durham, 1950	x	---	
Protothaca sp.	x	---	
Raeta ? sp.	---	x	
Sanguinolaria toulai Hertlein and Jordan, 1927	---	x	
Trachycardium sp.	---	x	

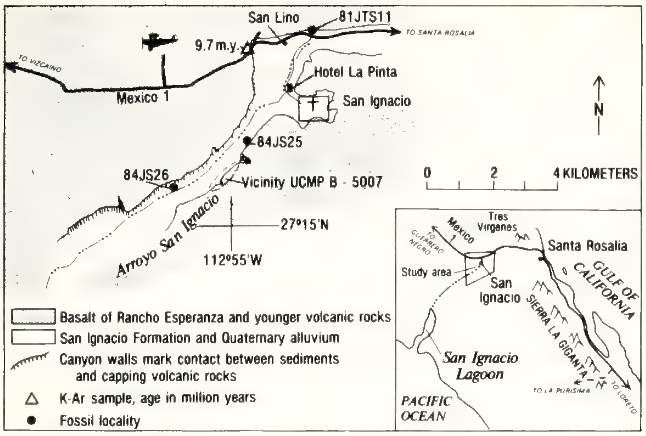

Fig. 3. The San Ignacio area, Baja California Sur, Mexico. Adapted from San Ignacio quadrangle G12A34, scale 1:50,000, and air photo 45A R405-30-9.

basalt of Rancho Esperanza (Sawlan and Smith, 1984). The upper part of the San Ignacio Formation near the turnoff to San Ignacio (81JTS11) consists of white bedded siltstones with few fossils, mainly elongate oysters, and it grades upward to nonmarine sediments that are covered by younger basalts.

Although the San Ignacio Formation is richly fossiliferous in the arroyo between 4 and 8 km southwest of town, rocky substrate forms are at present known only from sandy marls and sandstone beds on the southeast side of the canyon where they were collected from distances of 1.28 km (84JS25) and 4 km (UCMP locality B-5007) by road down the arroyo from the Hotel La Pinta. Calyptraeids were abundant in the sandier facies, not in living position but concentrated in randomly oriented clumps, associated with naticids, balanoid barnacles, and abundant Turritellas referred here to *Turritella* n. sp.?. Gregarious, usually offshore dwellers today, turritellids are sometimes concentrated on beaches as dead shells; the presence in the San Ignacio Formation of enormous numbers of juveniles as well as adults suggests an assemblage that lived close to the littoral rocky assemblage with which it is associated.

A locality on the northwest side of Arroyo San Gregorio at Rancho El Estribo (84JS26) lacks the sessile rocky substrate forms but has some of the same taxa as at the previous station (84JS25). *Turritella bosei* Hertlein and Jordan, 1927 occurs with, but mainly stratigraphically above, the other fossils, forming a monospecific ledge in the higher part of the exposed section. Above this ledge the formation grades into unfossiliferous, possibly nonmarine sediments capped by boulders of basalt of Rancho Esperanza. The contact between formations is obscured by talus, but regional relations suggest it is a disconformity with a period of erosion between the deposition of the fossils and extrusion of the basalts 10 m.y. ago (Sawlan and Smith, 1984).

Turritella bosei Hertlein and Jordan is probably related to the *Turritella abrupta* Spieker stock from the Miocene of Panama, Colombia, Ecuador, and Peru. Its occurrence in the upper San Ignacio Formation with a number of endemic mollusks permits correlation of this assemblage with those from the middle part of the Gatun Formation of Panama (Woodring, 1957), the Tuberá Group of northern Colombia (Anderson, 1929), the Angostura Formation of northwestern Ecuador (Olsson, 1964), and the Zorritos Formation of Peru (Spieker, 1922; Olsson, 1932). *Turritella bosei* Hertlein and Jordan, 1927 is abundant and all growth stages are represented; growth lines on gerontic body whorls suggest affinities with the *Turritella inezana* Conrad stock from the Miocene of California. Considered a member of the *Turritella ocoyana* Conrad stock by Merriam (1941), this taxon and the other Miocene turritellids from Baja California need a thorough systematic revision of the sort undertaken by Allison (1967) for the turritellids of Chiapas, Mexico.

Another San Ignacio Formation locality known from the literature and collections of Stanford University, the California Academy of Sciences, and the University of California, Berkeley is in the vicinity of Rancho San Angel (UCMP B-5031), about 24 km southwest of San Ignacio and accessible today from the road between Mexico 1 and Punta Abreojos. Taxa from locality UCMP B-5031 include many species found in Arroyo San Ignacio but no taxa from the penecontemporaneous Tortugas Formation of the nearby Vizcaino Peninsula.

Species from the San Ignacio Formation in Arroyo San Ignacio are listed in Table 1; representative taxa are illustrated on plates 2 and 3.

FOSSILS FROM THE LITTORAL ROCKY SUBSTRATE HABITAT

Mollusks that are not cemented to the substrate in the intertidal to sublittoral zone are rarely preserved as fossils, since they commonly live in areas of turbulent water that are usually far from sites of sedimentary deposition. Unless cemented, sessile forms tend to break and wash away before they can be buried by sediments.

Rocky substrate taxa recorded in the literature are mainly isolated specimens that were reworked and deposited with soft bottom species not far from their rocky habitats (as probably is the case for the San Ignacio Formation assemblage from 84JS25). The fossils from Purisima Vieja may be one of the oldest known rocky substrate assemblages preserved in living position.

It would be risky to assign the same names to taxa occurring thousands of miles apart because of the implications for geographic and phylogenetic connections. In this report many of the fossil mollusks from Baja California were identified from the literature; they are compared to (cf.) or related to (aff.) exotic taxa to avoid implying that a direct connection has been documented between biogeographic provinces or across boundaries between tectonostratigraphic terranes, pieces of the earth's crust with rocks and a geologic history different from those of adjacent areas. Rocky substrate taxa of Miocene age have been reported, although not as occurring in situ, in the following references: the Round Mountain Silt, Olcese and Jewett Formations, Kern County, California (Addicott, 1970); the Vaqueros Formation of California (Loel and Corey, 1932); the middle part of the Gatun Formation of Panama (Woodring, 1957-1982); the Zorritos and Tumbez Formations of Peru (Spieker, 1922; Olsson, 1932); the Angostura Formation of Ecuador (Olsson, 1964); the Tubera Group of northern Colombia (Anderson, 1929). There are many other examples recorded in the Tertiary Caribbean literature.

Shallow water rocky substrate species are difficult to identify because of the absence of color patterns and few indications of soft parts. Their shells tend to be undistinctive and intraspecifically variable in shape and form. The calyptraeids range widely in Holocene seas and may have been as cosmopolitan in the Miocene. A few specimens of patellacean limpets from the lower Isidro Formation (McLean and Hausback locality 383-19-7) are being studied by David R. Lindberg, University of California, Berkeley, for clues to the evolution of limpet morphology. The specimens reported on here are also available for specialists to study soft part traces that may be preserved in the shells.

REGIONAL SIGNIFICANCE OF THE ROCKY SUBSTRATE ASSEMBLAGES FROM PURISIMA VIEJA AND SAN IGNACIO, BAJA CALIFORNIA SUR

The middle Miocene mollusks from the upper parts of the Isidro and San Ignacio Formations indicate environmental conditions for this part of Baja California Sur before the formation of the Sierra la Giganta and the present Gulf of California. *Vermetus* and the air-breathing *Siphonaria* from Purisima Vieja mark a shoreline that was inundated during one brief rise in sealevel or downwarping of the area, as seen from the overlying sandstones containing *Melongena* sp. cf. *M. melongena* (Linnaeus, 1758). Marine regression and tectonic uplift exposed the area to nonmarine conditions for the last 14.5 m.y., during which time the sandstone and conglomerate of the Comondu Formation and overlying volcanic rocks were deposited. Basalt flows covering parts of the area are represented by mesa caps formed by subsequent dissection by streams that also deposited gravel terraces and exposed the marine rocks in the canyons.

The geology of the Baja California peninsula is only beginning to be studied within the context of plate tectonics, the theory of the earth's crust being composed of continent- and smaller-sized plates moving along, over or beneath each other, their edges marked by faults, spreading ridges, or deep trenches. Today the Baja California peninsula is part of the Pacific Plate, its boundary with the North American Plate being a series of faults extending from the San Andreas fault system of California through the Gulf of California. In places the Gulf of California is spreading apart at the same time the peninsula is inching northward with respect to the Mexican mainland. Until 7.5 m.y. ago, there was no structural trough in the Gulf of California and the Baja California peninsula was part of the North American Plate. Instead of the two plates sliding past one another, there was a different kind of motion, subduction: the Pacific Plate, then offshore to the west, was moving slowly eastward, dipping underneath the North American Plate at a rate of 6 cm per year. Maps showing these boundaries and data on which this history is based are given in Sawlan and Smith (1984).

The volcanism of which the dated flow at Purisima Vieja was a part was associated with the eastward subduction of the Pacific Plate beneath North America. When the Purisima Vieja mollusks were alive, just prior to this volcanic eruption, the intertidal assemblage exposed today in Arroyo San Gregorio (84JS16, 84JS17) lived on rocky ledges along the shore of a warm, shallow sea, unaffected by slabs of the earth's crust moving below.

The San Ignacio Formation mollusks underlie the basalt of Rancho Esperanza, which is believed to have been extruded from vents in the area of the present Gulf of California (Sawlan and Smith, 1984). The basalt has a radiometric age of approximately 10 m.y.; it overlies the uppermost nonmarine section of the San Ignacio Formation northeast of the town and the fossiliferous beds in the arroyo. This and younger basalts obscure the relationship between the San Ignacio Formation, with its neritic fauna of Caribbean and South American affinities, and the penecontemporaneous lower part of the Boleo Formation, which crops out only 50 km to the east in canyons north of Santa Rosalia. Significantly, the fossils from the San Ignacio Formation have affinities with taxa from Colombia and Peru while the fossils from the Boleo Formation, also a neritic deposit, are completely different and represent the earliest incursion of marine water in the Gulf of California in the early late Miocene (Smith, in preparation).

Evidence from geologic mapping suggests that parts of the Baja California peninsula may represent different tectonostratigraphic terranes, relicts of former tectonic plates or pieces of the earth's crusts having rock units and a geologic history distinct from those of adjacent areas (Blake *et al.*, 1984). When the physical setting of the Miocene tropical eastern Pacific is better known from paleomagnetic and other studies, molluscan distributions can be interpreted more accurately. Although some taxa would have had planktonic larvae capable of long distance dispersal, others probably developed directly, as in the case of *Melongena* (Clench and Turner, 1956). The distributions of nonplanktonic taxa are a potentially useful tool for distinguishing molluscan distribution patterns due to free-swimming larvae from those modified by plate motion. Although terranes may have moved relatively short distances within the geographic ranges of many taxa, increments of time can be measured by the evolution of key index species. Such fossils will provide finer resolution of time scales and information on the geographic origin of terranes that have been identified by geologic mapping and paleomagnetic data.

ABBREVIATIONS

CAS: California Academy of Sciences, Golden Gate Park, San Francisco, California 94118; LSJU: Leland Stanford Junior University, collections now at the California Academy of Sciences; M number: U. S. Geological Survey locality, Cenozoic register, Menlo Park, California; UCMP: University of California Museum of Paleontology, Berkeley, California 94720; USGS: U. S. Geological

Survey; USNM: U. S. National Museum.

Abbreviations used in locality data and plate explanations: RV: right valve; LV: left valve; ht.: height in cm.

The specimens reported on here will be deposited upon publication at the U.S. National Museum, Washington, D.C. and the Instituto de Geologia, Mexico City.

LOCALITY DATA

Judith T. Smith localities

81JTS8 [=M8648] San Isidro, Baja California Sur. La Purisima quadrangle, G12A86, 1:50,000. Air photo 45A R516-21-27. North bank of stream in Arroyo la Purisima where road from San Isidro to Paso Hondo crosses the stream. Isidro Formation, early Miocene. Abundant fossils, including echinoids and *Spondylus scotti* Brown and Pilsbry, 1913. J.T. Smith and J.G. Smith collectors, April 3, 1981.

81JTS11 [M8649] San Ignacio, B.C.S. North side of Mexico 1 at turnoff to San Ignacio (Km 73.5). White bedded siltstone with pink air fall pumice and tuffaceous interbeds; abundant elongate oysters and other poorly preserved clams. San Ignacio Formation, late middle Miocene. J.T. Smith and J.G. Smith collectors, April 4, 1981.

81JTS11a [M8650] San Lino, just south of Mexico 1, ½ km west of turnoff to San Ignacio. Same rocks, fossils, collectors as 81JTS11.

84JS16 [M8651] Paso Hondo quadrangle, G12A76, 1:50,000 ("Pozo Hondo" of unpublished provisional map), air photo 46A R510-15-26. Just north of Purisima Vieja, the palm grove in a tributary to Arroyo San Gregorio, 15 km by road northwest of San Isidro and 5 km due south of Paso Hondo. West of the road, east side of main stream bed in Arroyo San Gregorio, on a low bench about a meter above the stream. Coarse laminated sandstone, upper part of the Isidro Formation, middle Miocene. Rocky substrate mollusks. J.T. Smith and T.M. Cronin, collectors, March 24, 1984; = Cronin ostracod samples 84TC67, 68, and 69.

84JS17 [M8652] Across Arroyo San Gregorio from 84JS16, at the base of the northern of the two knobs that stand above the west side of the arroyo. 1-2 m above the stream bed. Sandstone and tuffaceous sediments, coquina layers and burrows; grades upward to nonmarine sandstone and conglomerate of the Comondu Formation. Isidro Formation, upper part, same stratigraphic level but north of McLean and Hausback locality 383-11-2, and immediately upsection from 84JS16. J. T. Smith and T.M. Cronin, collectors, March 24, 1984. = Cronin ostracod samples 84TC70-72.

84JS25 [M8653] San Ignacio quadrangle, G12A34, 1:50,000. Air photo 45A-R485 30-9. Southeast side of Arroyo San Ignacio, 1.28 km along an unmarked dirt road that leaves the road between Mexico 1 and the town square near the Hotel La Pinta; south of an unmarked road to La Candeleria camp. Downstream end of section of arroyo wall marked by a prominent white ledge of sandy marl and sandstone, capped by talus of basalt of Rancho Esperanza (Sawlan and Smith, 1984). Highly fossiliferous, abundant *Turritella* and *Crucibulum*. San Ignacio Formation, middle Miocene. J.T. Smith and T.M. Cronin collectors, March 27, 1984. = Cronin localities 84TC93-99.

84JS26 [M8654] Northwest side of Arroyo San Ignacio, 3.37 km downstream from road between Mexico 1 and the town square. 3.5 km due south of the turnoff to the airport on Mexico 1, on air photo 45A R485 30-9. Small gully north of Rancho El Estribo, 2 km by road downstream from 84JS25. White sandstone and marl, some of which is well indurated; capped by boulders of basalt of Esperanza, which has been radiometrically dated at 10 m.y. (Sawlan and Smith, 1984). A ledge of *Turritella bosei* Hertlein and Jordan in the upper part of the highly fossiliferous section. J.T. Smith and T.M. Cronin, collectors, March 28, 1984. = Cronin localities 84TC100-104.

McLean and Hausback localities

383-11-1 Paso Hondo quadrangle, G12A76, 1:50,000. Air photo 46A R510-15-26. About ½ km up Arroyo San Gregorio from the palm grove at Purisima Vieja and at the base of the southern of the two buttes above the western wall of the arroyo. Basalt flow interbedded in nonmarine sandstone of the lower part of the Comondu Formation, about 30 m above marine mollusks of the upper Isidro Formation. Radiometric age of 14.5 m.y. (Hausback, 1984). Hugh McLean and B.P. Hausback collectors, March 11, 1983.

383-11-2 [M8655] Same as 383-11-1 but marine sediments about 30 m stratigraphically below the basalt flow. Isidro Formation, upper part, middle Miocene. Hugh McLean and B.P. Hausback collectors, March 11, 1983.

383-18-2 [M8656] La Purisima quadrangle, G12A86, 1:50,000. Air photo 46A R516-26-27. West bank of Arroyo San Gregorio, north and upstream from junction of the road between La Purisima and San Juanico with the arroyo. Isidro Formation, early Miocene. Hugh McLean and B.P. Hausback, collectors, March 18, 1983.

383-18-6 [M8657] Southwest ¼ Paso Hondo quadrangle, G12A76, 1:50,000. Air photo 46A R510-11-26. 26º16′20″N, 112º18′00″W. West bank of Arroyo Mezquital. Isidro Formation, early early Miocene. Hugh McLean and B.P. Hausback collectors, March 18, 1983.

383-19-7 [M8658] Paso Hondo quadrangle, G12A76, 1:50,000. Air photo 46A R510-11-26. 26º16′20″N, 112º18′00″W. South side of Arroyo Mezquital. Isidro Formation, rocky substrate fossils. Hugh McLean and B.P.Hausback, collectors, March 19, 1983.

482-28-3-8 [M8659] Purisima quadrangle, G12A86, 1:50,000. Arroyo La Purisima, La Ventana area, 26º16′20″N, 112º11′02″W. Rhyolite tuff in upper part of San Gregorio Formation dated at 23.4 ± 0.3 m.y., providing the oldest absolute age estimate for the lower part of the overlying Isidro Formation. Hugh McLean and B.P. Hausback collectors, April 28, 1982.

Sawlan and Smith (1984) locality

82BMS591 San Ignacio quadrangle, G12A34, 1:50,000. Roadcut on Mexico 1 at San Lino, [km 74] ½ km west of turnoff to San Ignacio. Basalt of Rancho Esperanza, radiometric age of 9.7 ± 0.29 m.y. Overlies the marine fossiliferous San Ignacio Formation. J.G. Smith and M.G. Sawlan, collectors, 1982.

Museum locality numbers

CAS 54066 La Purisima quadrangle, G12A86, 1:50,000. Arroyo San Gregorio, side of the canyon where road from La Purisima to San Juanico enters the arroyo. Isidro Formation, early Miocene. O.E. Bowen collector, Aug. 1973.

LSJU 66 Arroyo San Ignacio, 8 km southwest of the town of San Ignacio. San Ignacio Formation, middle Miocene (Ysidro Formation of collector B.F. Hake, March 9, 1921).

UCMP A-601 La Purisima area, Baja California, "Turritellas below other zones, canyon del Cordon" [de cardones, 8 km downstream from Purisiam Vieja in Arroyo San Gregorio, according to Beal's field sheet] of collector W.L. Watts (Merriam, 1941; Loel and Corey, 1923).

UCMP B-5007 Arroyo San Ignacio, about 4 km by road from San

Ignacio toward San Angel via San Sabas. South slope of the arroyo in prominent exposures about ¼ mile (.4 km) south of road, about ¼ miles (.4 km) along the cliff. 75′ (23 m) of flat-lying white sand and siltstone capped by basalt. At least 4 or 5 marine invertebrate horizons with abundant *Turritella* [the species here referred provisionally to *Turritella* n. sp.?] in bed at base. Ysidro Formation [San Ignacio Formation] of collectors E.C. Allison and F.H. Kilmer, July 13, 1957.

UCMP B-5031 San Ignacio quadrangle, G12A34, 1:50,000. 15-20 km west of San Ignacio, about 1.5 km by road southeast of Rancho San Angel on old road to San Juan, San Sabas, and San Ignacio. South bank of narrow arroyo, about 150′ west of road in about 15′ of flat-lying very fossiliferous grey limy sandstone. Ysidro Formation [San Ignacio Formation] of collectors E.C. Allison and F.H. Kilmer, 1957.

USGS 9157 Paso Hondo quadrangle, 1:50,000. Arroyo San Gregorio [Beal's Arroyo Guajademi], "between Paso Hondo and Purisima Vieja where the trail cuts hill in turn at stream," according to collector W.S.W. Kew, 1920. Isidro Formation, early Miocene. Specimens and matrix from this locality match those from locations in the lower, early Miocene part of the Isidro Formation and probably came from the section downstream from the palm grove at Purisima Vieja.

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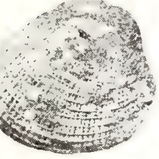
►

PLATE 1. Middle Miocene mollusks from the upper Isidro Formation, Purisima Vieja, Baja California Sur, Mexico. **Figs. 1-19. 1.** *Protothaca* sp. Hypotype USNM 387586, loc. 84JS16. Ht. 1.9 cm, lenth 2.0 cm. **2, 2a.** *Theodoxus* sp. {*Neritina* of authors}. Side, apertural views, hypotype USNM 387587, loc. 84JS16. Ht. 1.4 cm, width 1.6 c.m. **3.** *Vermetus* sp. cf. *V. contortus* (Carpenter, 1857). Hypotype USNM 387588, loc. 84JS17. Length of colony, 3 cm. **4, 8.** *Melongena* sp. cf. *M. melongena* (Linnaeus, 1758). Apical view showing excurrent notch, side view, hypotype USNM 387589, loc. 84JS17. Ht. 7.3 cm (incomplete). **5.** *Siphonaria maura pica* Sowerby, 1835. Hypotype USNM 387590, loc. 84JS16. Length 3.6 cm, width, 3.2 cm. **6.** *Hipponix pilosus* (Deshayes, 1832). Hypotype USNM 387591, loc. 84JS16. Length 1.5 cm, width 1.4 cm. **7.** *Anadara* sp. cf. *A. (Cunearca) nux* (Sowerby, 1833). Hypotype USNM 387592, loc. 84JS17. Ht. 1.1 cm, length 1.8 cm. **9.** *Turritella altilira* Conrad, 1857. Hypotype USNM 387593, McLean and Hausback loc. 383-11-2. Ht. 3.9 cm (incomplete). **10, 11.** *Turritella* sp. cf. *T. crocus* Cooke, 1919. Fig. 10, apertural view, hypotype USNM 387594, loc. 84JS17. Ht. 3 cm (incomplete); Fig. 11, apertural view, voucher specimen CAS G61398, loc. CAS 54066, Arroyo San Gregorio near the road to San Juanico; ht. 4 cm (incomplete). Isidro Formation, Miocene. **12.** *Plicatula* sp. cf. *P. inezana* Durham, 1950. Hypotype USNM 387595, loc. 84JS17. Maximum dimension 3 cm. **13.** *Trochita* sp. cf. *T. radians* Lamarck of Arnold and Anderson (1907). Hypotype USNM 387596, loc. 84JS16. Diameter 3.4 cm. **14.** *Calyptraea* sp. Hypotype USNM 387597, loc. 84JS16. Diameter 3.2 cm (incomplete). **15, 16.** *Trochita trochiformis* (Born, 1778). Side, apical views, hypotype USNM 387598, McLean and Hausback loc. 383-19-7, Isidro Formation, Miocene. Ht. 2.2 cm, diameter 4.1 cm (incomplete). **17, 18.** *Tegula* sp. Fig. 17, basal view, hypotype USNM 387599, loc. 84JS16. Diameter 2.1 cm. Fig. 18, side view showing puckers below suture, hypotype USNM 387600, loc. 84JS16, ht. 2.7 cm (incomplete), width 2.9 cm. **19.** *Turritella* sp. cf. *T. altilira* Conrad, 1857. Hypotype USNM 387601, loc. 84JS17. Ht. of juvenile fragment 2.5 cm.

PLATE 2. Late middle Miocene mollusks from the San Ignacio Formation, Arroyo San Ignacio, Baja California Sur, Mexico (locality 84JS25 unless noted). **Figs. 1-19. 1,2.** *Strombina* sp. Fig. 1, side view, hypotype USNM 387602, ht. 2.6 cm. Fig. 2, apertural view, hypotype USNM 387603, ht. 2.3 cm. **3.** *Calliostoma hannibali* Hertlein and Jordan, 1927. Apertural view of nonumbilicate taxon, hypotype USNM 387604, ht. 1.2 cm, width 1.2 cm. **4.** *Nassarius* sp. cf. *N. versicolor* (C.B. Adams, 1852). Hypotype 387605, ht. 1.3 cm. **5, 6.** *Terebra burckhardti* Hertlein and Jordan, 1927. Fig. 5, abapertural view, holotype LSJU 5152, loc. LSJU 66, ht. 2.5 cm; fig. 6, hypotype USNM 387606, loc. UCMP B-5007, ht. 3 cm (incomplete). **7.** *Neverita (Glossaulax)* sp. cf. *N. (G.) andersoni* (Clark, 1918). Apertural view, hypotype USNM 387607, ht. 1.7 cm, width 1.8 cm. **8, 9.** *Crucibulum inerme* Nelson, 1870. Fig. 8, apical view, hypotype USNM 387608, length 3.4 cm (incomplete), width 3 cm; fig. 9, apertural view, hypotype USNM 387609, length 4.2 cm, width 3 cm (incomplete). **10.** *Crepidula* sp. Hypotype USNM 387610, ht. 3.5 cm (incomplete). **11.** *Macron hartmanni* Hertlein and Jordan, 1927. Holotype LSJU 5146, loc. LSJU 66, ht. 4.7 cm, width 2.9 cm. **12.** *Drillia (Clathrodrillia)* sp. Apertural view, hypotype USNM 387611, ht. 3.2 cm (incomplete). **13.** *Turritella costaricensis* Olsson, 1922. Hypotype USNM 387612, ht. 4.7 cm (incomplete). **14, 15.** *Turritella* n. sp.? Fig. 14, hypotype USNM 387613, ht. 4.5 cm (incomplete); fig. 15, hypotype USNM 387614, ht. 5.3 cm (incomplete). **16, 17.** *Crassilabrum wittichi* (Hertlein and Jordan, 1927). Apertural, abapertural views, hypotype USNM 387615, ht. 5 cm (incomplete), width 4 cm. **18.** *Knefastia* sp. Apertural view, hypotype USNM 387616, ht. 5.2 cm. **19.** *Turritella bosei* Hertlein and Jordan, 1927. Hypotype USNM 387617, from the highest fossil ledge at 84JS26. Ht. 8 cm (incomplete).

PLATE 3. Late middle Miocene mollusks from the San Ignacio Formation, Arroyo San Ignacio, Baja California Sur, Mexico. **Figs. 1-15. 1,2.** *Mytilus* sp. cf. *M. canoasensis vidali* Ferreira and Canha of Woodring, 1973. Fig. 1, hypotype USNM 387618, length 5.5 cm (incomplete); fig. 2, hypotype USNM 387619, length 4.7 cm (incomplete). Loc. 84JS25. **3, 4.** *Lucina (Lucinisca)* sp. LV. hypotype USNM 387620, seen in different light. Loc. 84JS25, ht. 1.8 cm, length 1.9 cm. **5.** *Choromytilus* sp. cf. *C. palliopunctatus* (Carpenter, 1857). Hypotype USNM 387621, loc. 84JS25. Length 4.6 cm. **6.** *Cyclinella* sp. Hypotype USNM 387622, loc. 84JS25. Ht. 2.9 cm, length 3 cm. **7, 12.** *Ostrea* sp. a. Fig. 7, internal view, LV, hypotype USNM 387623, loc. 81JTS11a, longest dimension 14.5 cm; fig. 12, external view, hypotype USNM 387624, loc. 81JTS11, longest dimension 9.2 cm (incomplete). **8, 9.** *Chione (Chione) richthofeni* Hertlein and Jordan, 1927. RV, posterior view, holotype LSJU 5143, loc. LSJU 66, ht. 4.9 cm, length 5 cm. **10, 13.** *Cypraea amandusi* Hertlein and Jordan, 1927. Side, apertural views, holotype LSJU 5145, loc. LSJU 66, length 5.9 cm, width 4.7 cm. **11.** *Chione (Chionopsis)* sp. LV, hypotype USNM 387625, loc. 84JS25. Ht. 3.7 cm, length 3.4 cm. **14.** *Amiantis* sp. CAS voucher specimen 61345, loc. LSJU 66, ht. 6.7 cm, length 8.2 cm. **15.** *Cymia heimi* Hertlein and Jordan, 1927. Holotype LSJU 5139, loc. LSJU 66, ht. 8 cm.

Plate 1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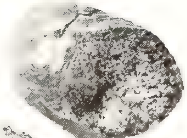
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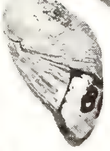
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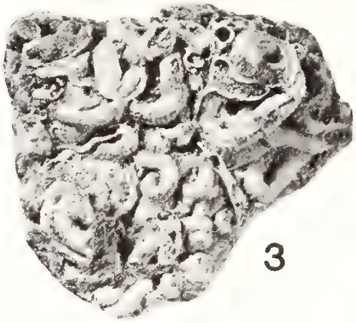
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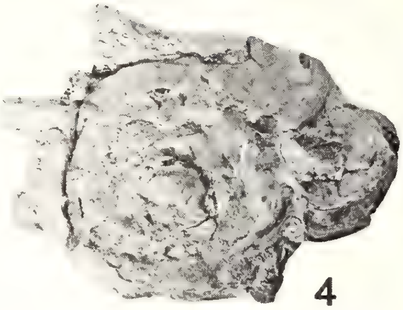
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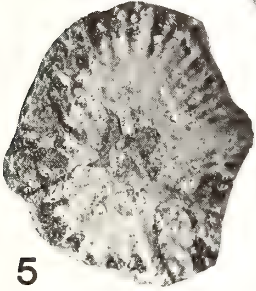
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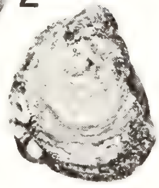
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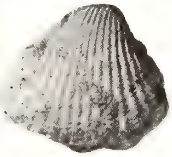
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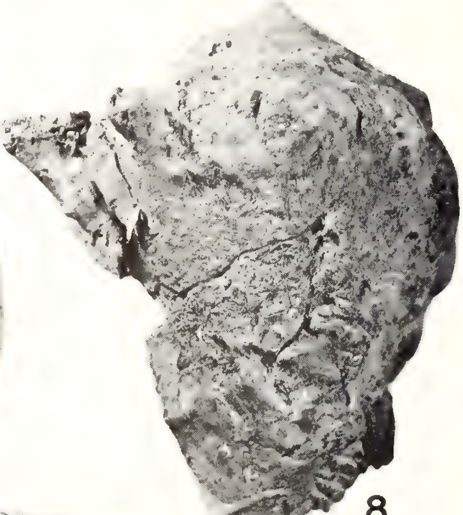
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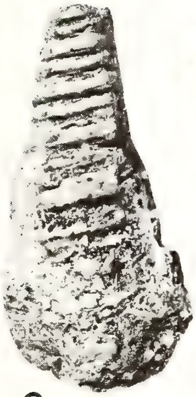
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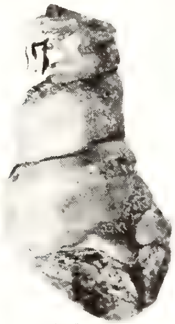
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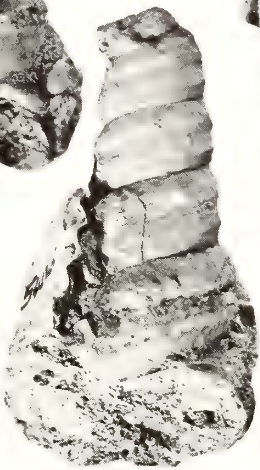
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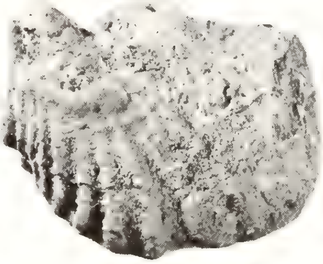
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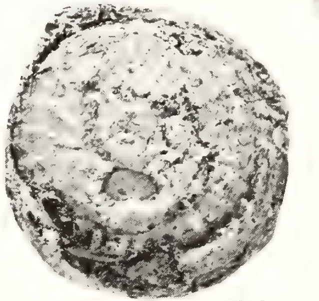
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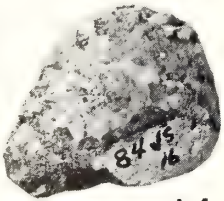
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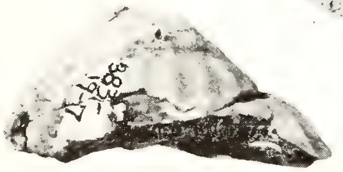
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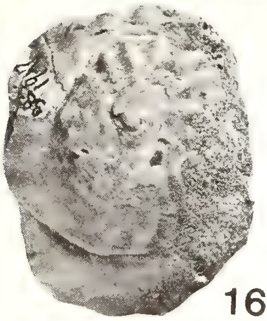
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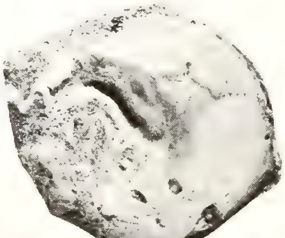
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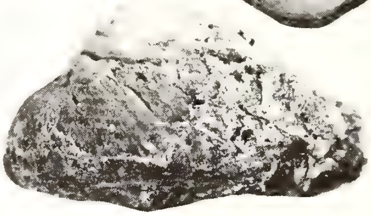
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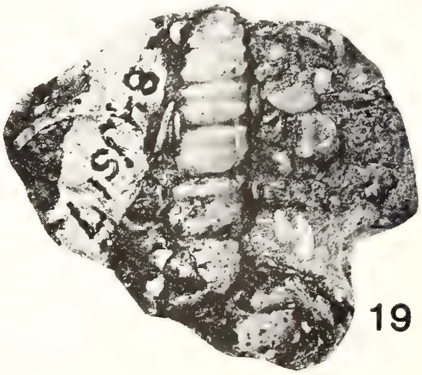
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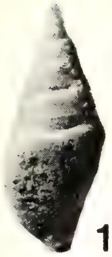
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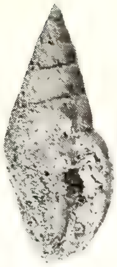
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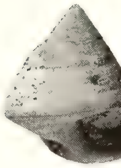
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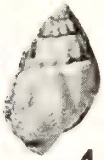
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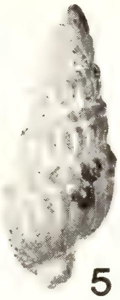
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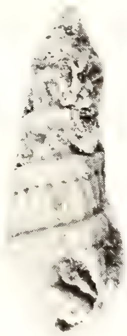
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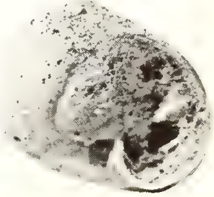
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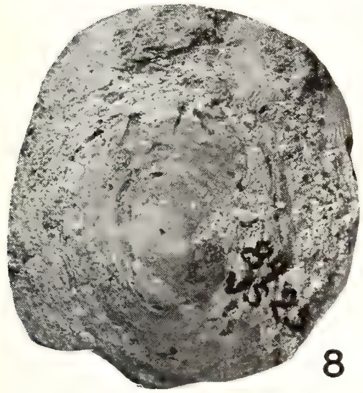

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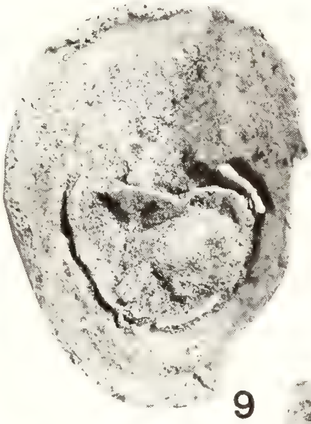
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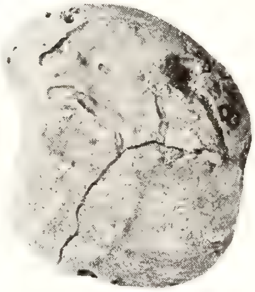
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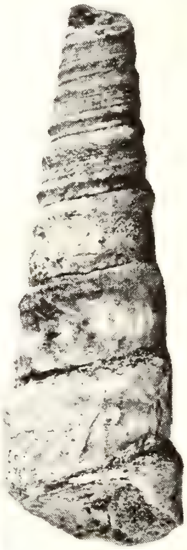
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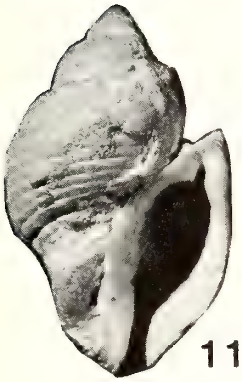
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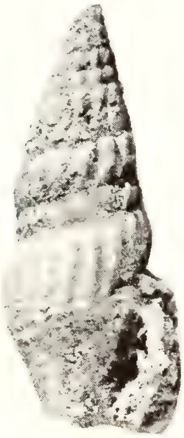
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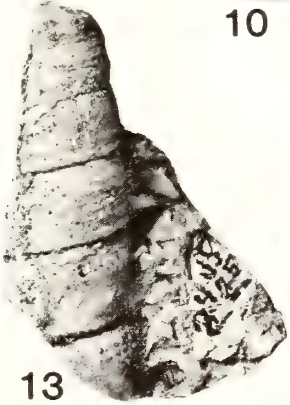

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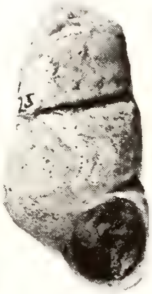

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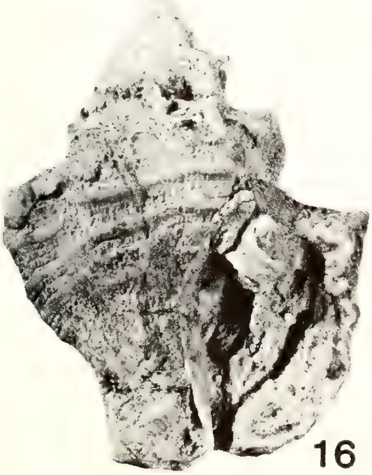
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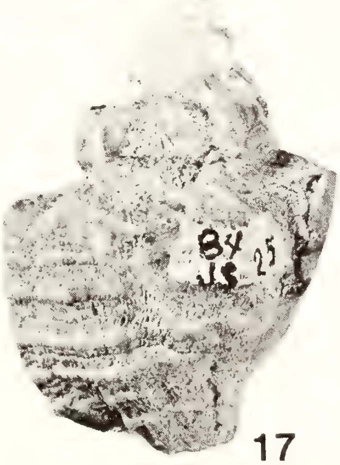

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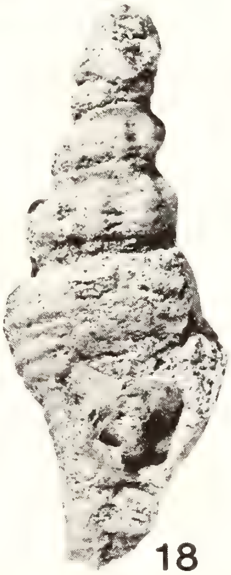
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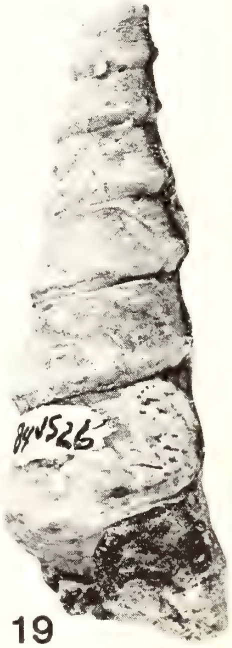

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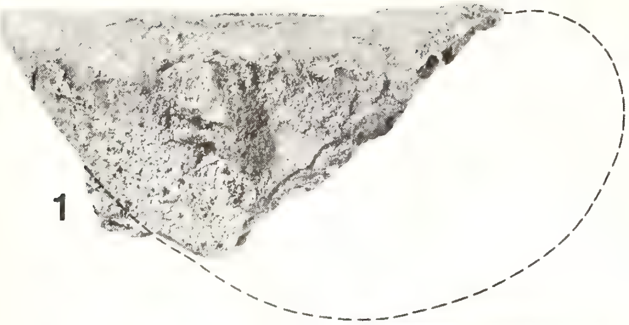
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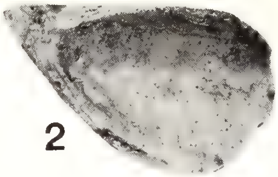
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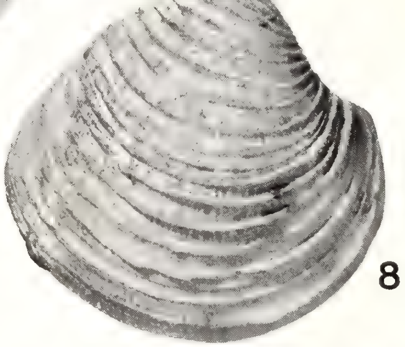
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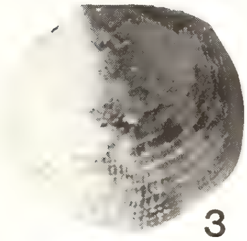
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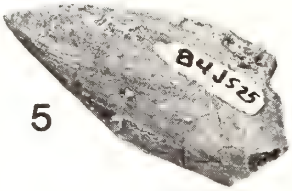

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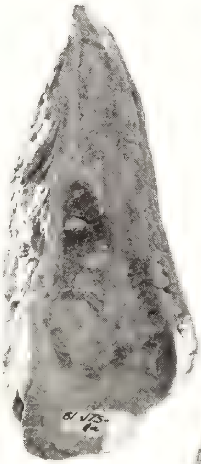

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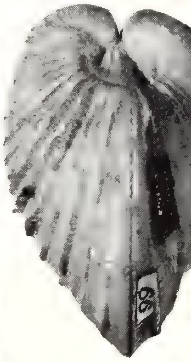

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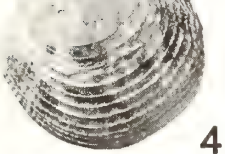
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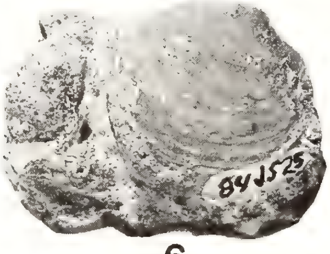

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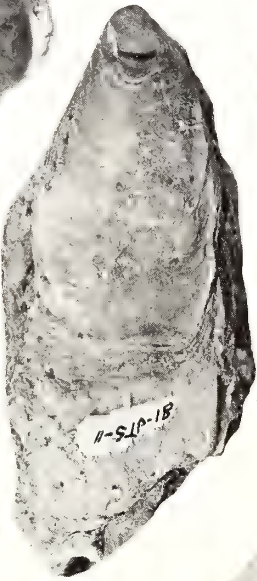

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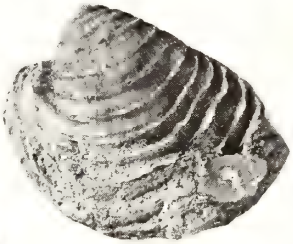
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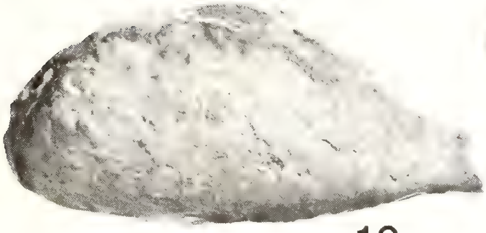
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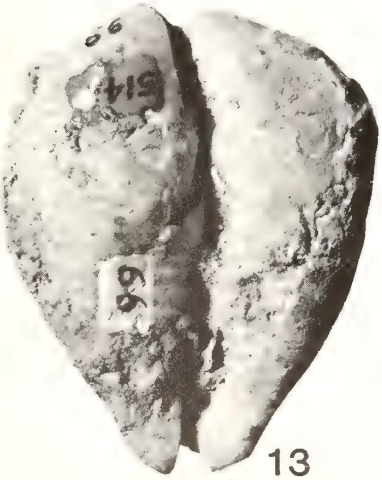

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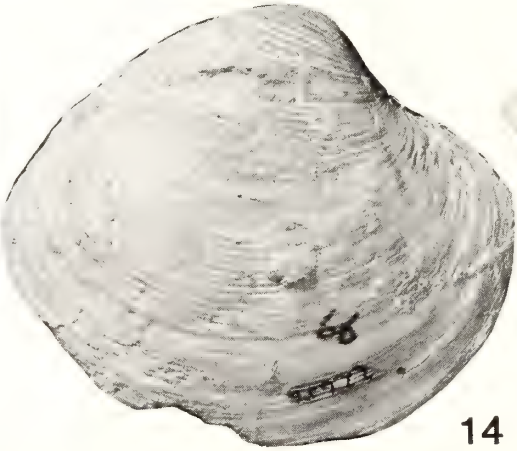

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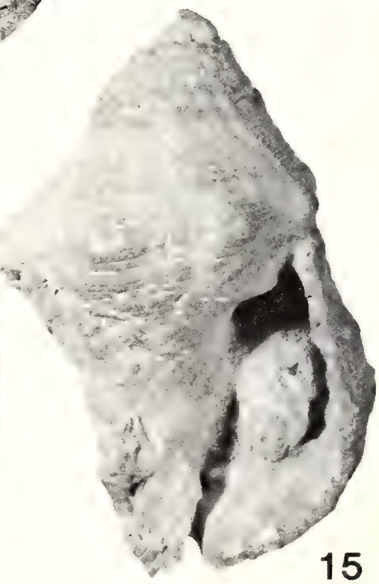
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THE STOMACH ANATOMY OF SOME EASTERN NORTH AMERICAN MARGARITIFERIDAE (UNIONOIDA: UNIONACEA)

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ABSTRACT

Previous investigations on the stomach anatomy of various unionacean species have revealed similarities to that of *Neotrigonia* sp., a member of the marine Trigonioida, a group believed ancestral to the Unionoida. The present study investigated the stomach anatomy of the most primitive unionacean family, the Margaritiferidae. The morphology of the margaritiferid stomach is variable and in some ways appears intermediate between trigonids and other unionaceans. The overall similarity of stomach morphology among trigonids, margaritiferids, and other unionceans provides additional evidence of a phylogenetic relationship between the Trigonioida and Unionacea. Although distinct morphological patterns are present within *Margaritifera margaritifera, M. marrianae,* and *Cumberlandia monodonta,* none of these suggests anything greater than species-level differences.

The bivalve stomach has received considerable study (Purchon, 1977). Representative families of each subclass have been investigated and major morphological patterns of stomach anatomy have been demonstrated. However, disagreement exists as to the interpretation of various stomach morphologies in some groups (Purchon, 1958, 1960;Dinamani, 1967). Within the polysyringian (= eulamellibranch = synaptorhabdic) order Unionoida, superfamily Unionacea, stomach anatomies of the genera *Anodonta, Lamellidens,* and *Lampsilis* (Unionidae) and *Velesunio* (Hyriidae) have been studied (Gutheil, 1912; Graham, 1949; Owen, 1955; Purchon, 1958; Dinamani, 1967, Kat 1983a, b). The unionid stomach appears to be fairly uniform in morphology, and the stomach of the single hyriid form examined was similar to unionid species (Purchon, 1958). However, Kat (1983a,b) noted differences in the shape and relative proportions of stomach structures among species of the genera *Anodonta* and *Lampsilis*. Kat (1983a,b) further maintained that species groups within each genus could be diagnosed using stomach anatomy in conjunction with other morphological and non-morphological characters.

The anatomy of the stomach of the Margaritiferidae, the third presently recognized family in the Unionacea, is unknown. Other anatomical characters suggest that the Margaritiferidae is the most primitive group within the Unionoida (Ortmann, 1911; Heard, 1974; Smith, 1979). Furthermore, the Margaritiferidae possess specific anatomical traits that link unionoids with marine Trigonioida (Gould and Jones, 1974; Smith, 1980; 1983). On the basis of shell characteristics the trigonioids have been implicated as the likely ancestral group to the unionoids (Cooke, 1927; Newell and Boyd, 1975). The present study was undertaken to determine if stomach anatomy would provide additional information on the relationships between the Margaritiferidae and other unionacean families and the Recent marine trigonids. It was hoped these investigations would also present a better understanding of the evolutionary and systematic relationships of the genera *Margaritifera* and *Cumberlandia.*

The stomach morphology of the following three representative species of the Margaritiferidae was examined: *Margaritifera margaritifera* (L.), a species occurring in eastern North America and Europe; *M. marrianae* Johnson, a species with a very restricted distribution in the Gulf coast region; and *Cumberlandia monodonta* (Say), a widely distributed species in east-central North America and one showing the greatest apparent morphological divergence among the more fully described margaritiferid species.

MATERIALS AND METHODS

A total of 21 specimens representing the three margaritiferid species mentioned above were

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dissected. Of these 41 specimens, six (*M. margaritifera*) were used for initial exploratory dissections and histological examination and were not included in the morphological analysis. All specimens dissected had been fixed in 10% formalin and stored in either 50% isopropyl alcohol or 70% ethyl alcohol. Specimens were preserved unrelaxed, or were preserved following freezing, or were relaxed prior to preservation. Methods of preservation, although influencing the shape of the stomach, did not affect the appearance of internal structures. All material relevant to this study, except for a few specimens that were loaned to me by Mr. Tom Freitag, is presently housed in the Invertebrate Division of the Museum of Zoology, University of Massachusetts, Amherst (UMA). The following list provides particulars of specimens used in this study.

Margaritifera margaritifera:

UMA MO. 683, MA, Hampshire County, Amherst, Cushman Brook, 3 September, 1974. Four specimens.

UMA MO. 1066, RI, Washington County, Exeter, Queen River, 25 August, 1978. Three specimens.

UMA MO. 1273, PA, Schuylkill County, Ryan, Locust Creek, 13 March, 1982 and 23 June, 1983. Five specimens.

UMA MO. 1347, MA, Hampden County, Palmer, Quaboag River, 20 October, 1982. Four specimens.

UMA uncataloged, MA, Hampshire County, Amherst, Fort River, 1 August, 1984. Three specimens.

Margaritifera marrianae:

UMA MO. 1248, AL, Crenshaw County, Rutledge, Horse Creek, 2 August, 1981. Six specimens.

Cumberlandia monodonta:

UMA MO. 1143, TN, Hawkins County, Kyles Ford, Clinch River, 7 and 12 August, 1979. Five specimens.

UMA MO. 1425 and T. Freitag (uncat.), MO, St. Louis County, Eureka, Meramec River, 28 October, 1982. Three specimens.

UMA MO. 1426, IL, Rock Island County, Rock Island, Mississippi River, 18 August, 1978. One specimen.

T. Freitag (uncat.), IA, Mercer County, Muscatine, Mississippi River, 19 June, 1978. One specimen.

In addition to the margaritiferid specimens, four specimens of *Anodonta implicata* Say and a single specimen of *Lampsilis radiata* (Gmelin) were dissected for inspection of stomach floor morphology. These dissections were to familiarize myself with the structures and terminology discussed by Kat (1983a,b). These dissections were also used to compare with Kat's (1983a,b) observations and with my own dissections of margaritiferid stomachs.

Stomachs and surrounding visceral tissue were removed from specimens. The isolated tissue containing the stomach was then dissected from the dorsal side (nearest to the hinge) and examined using a stereozoom binocular dissecting microscope. The areas of ciliated ridges lining the internal surfaces of the stomach were assumed to represent the "sorting areas" of previous investigators. No attempt was made to determine the function of the extensive ciliary systems (sorting areas) of stomachs of live animals. The term "sorting area" is used in subsequent descriptions to identify specific areas in which ciliated ridges are present.

The terminology of the various structures of the bivalve stomach has not been as consistent as that of other major organs of the pelecypod body. This is particularly true in the sroting areas covering the inner stomach surfaces. The situation will not be easily remedied, certainly not by proposing new terms. Therefore, this paper will follow, as closely as possible and where applicable, Purchon's (1958) terminology for *Anodonta cygnea* (L.).

RESULTS

GENERAL STOMACH ANATOMY

In the margaritiferid species examined the stomach is situated dorsally and anteriorly in relation to the visceral mass. The general shape of the esophagus and stomach and the external morphology of the stomach roof is shown in figure 1. The stomach is an enlarged sac surrounded laterally and ventrally by digestive gland (LLD, RLD, PLD). Dorsally, the right and left lobes of the digestive gland extend over the roof but do not meet anteriorly. The esophagus (OES) is a flattened, short tube lying beneath the anterior adductor muscle and resting between and on the visceral muscles and the anterior muscles of the foot (APR). The lateral margins

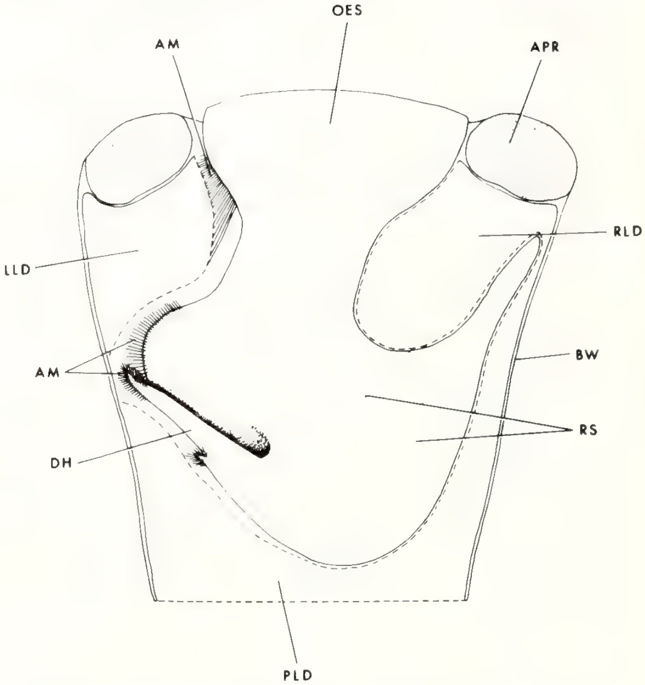

Fig. 1. The generalized roof of the margaritiferid stomach and associated organs and structures. Dashed lines represent cuts in tissue. Abbreviations: AM = attachment muscle, APR = anterior pedal retractor muscle, BW = body wall, DH = dorsal hood, LLD = left lobe of digestive gland, OES = esophagus, PLD = posterior lobe of digestive gland, RLD = right lobe of digestive gland, RS = ridges delimiting principal sorting areas of roof. Horizontal field width = 13 mm.

of the esophagus are held in place by bands of attachment muscle (AM). The morphology of the stomach roof is in general agreement with other unionaceans (Graham, 1949; Purchon, 1958; Dinamani, 1967; Kat 1983a,b). The dorsal hood (DH) represents the most outstanding feature of the roof and is supported along with other portions of the left wall by attachment muscles (AM). Two prominent ridges (RS) are visible through the roof. These ridges delimit the principal sorting areas of the interior surface of the roof.

Internally (Fig. 2), the stomach floor, and in particular the lateral and posterior walls, are generally similar to other unionaceans. The gastric shield, not shown in the figure, shows no differnces from *Anodonta* spp. (Graham, 1949; Purchon, 1958) or *Lamellidens* sp. (Dinamani, 1967). The same is true for the posterior wall and the left wall, with some exceptions depending upon the species investigated. The right embayment (RE) increases the area of the stomach. Ducts leading to the digestive diverticula originate from the anterior right and left walls (LAD, RD), and from a pocket in the left posterior wall (LPD) ventral and posterior to the dorsal hood (DH) and a shallow left embayment (LE). The right wall, particularly the right sorting area (RSA), combining the "longitudinal ridge" (Purchon, 1958) and the "anterior fold" (Dinamani, 1967), showed considerable variation among the species studied. The stomach floor contains a major typhlosole (T) which arises from the midgut (MG) and shows a strong fold and a swollen "conical mound" (Purchon, 1958) characteristic of other unionaceans at the apex of the fold. The typhlosole then proceeds to the left where it variously enters or terminates at the opening of the left anterior digestive duct system (LAD). The minor typhlosole (MT) arises near the major typhlosole and curves to the right posterior to the right digestive duct (RD). The ventral embayment (VE) is rather uniform throughout the species examined and represents a ventral extension of the posterior stomach floor. No comparison can be made with other unionacean species studied as this structure was not discussed by previous investigators. No consistent differences were detected between margaritiferid species and the few unionid species examined in this study.

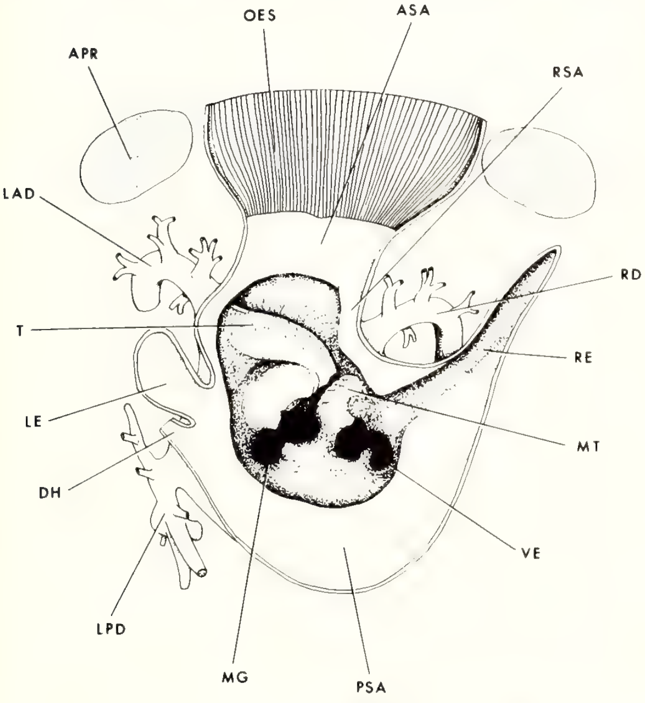

Fig. 2. Generalized interior and digestive duct systems of the margaritiferid stomach. Abbreviations: APR = anterior pedal retractor muscle, ASA = anterior sorting area, DH = dorsal hood, LAD = left anterior duct system, LE = left embayment, LPD = left posterior duct system, MG = midgut and style sac, MT = minor typhlosole, OES = esophagus, PSA = posterior sorting area, RD = right duct system, RE = right embayment, RSA = right sorting area, T = major typhlosole, VE = ventral embayment. Horizontal field width = 13 mm.

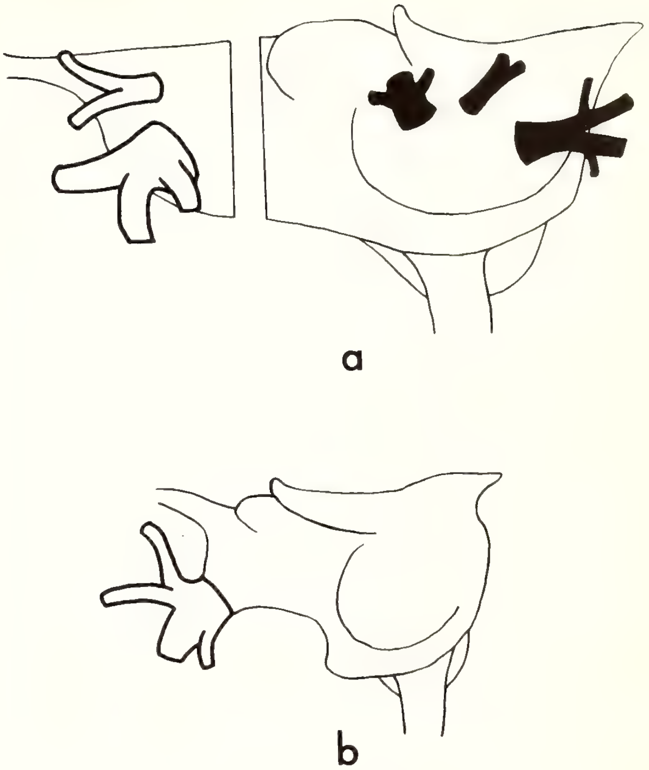

Fig. 3. Diagrammatic representation of the left anterior (open, heavy lines) and posterior (solid) duct systems of the stomach showing maximum variation observed: a, composite of different specimens of *M. margaritifera*; b, specimen of *M. marrianae*. Horizontal field width = 17 mm.

Anteriorly, the termination of the esophagus (OES) is marked by a rim, as is the case in other unionaceans. The area immediately posterior to the esophageal rim, the anterior sorting area (ASA), is variously developed in examined margaritiferid species. The interior floor surface is covered with extensive sorting fields, which Purchon (1958) differentiated and identified. These sorting fields are associated with the typhlosoles, duct openings, and embayments. No special differences were noted between margaritiferid species and other unionacean species previously studied.

SPECIES DESCRIPTIONS

MARGARITIFERA MARGARITIFERA. The stomach of this species demonstrated the greatest dissimilarity with the typical unionacean stomach as described by previous investigators. Whereas in other unionceans in which the major typhlosole always terminates well inside the left anterior duct opening, the major typhlosole in *M. margaritifera* did not consistently enter the duct system. This condition is somewhat dependent on the population studied. In individuals of one population sampled, the major typhlosole entered the duct. In contrast, in another population the organ terminated near the entrance of the duct. Furthermore, a few populations sampled contained animals in which both conditions existed.

The right duct system was always observed to arise from a single opening in the right wall of the stomach. The left anterior duct system usually arose from a single opening in the left wall, as in other unionaceans, except perhaps *Lamellidens* sp. (Dinamani, 1967), occasionally, two openings occurred (Fig. 3a). Posteriorly, the left posterior duct system commonly had a single opening, which branched into anterior and posterior trunks (see Fig. 2). Exceptions rarely occurred in which certain specimens showed multiple openings (Fig. 3a).

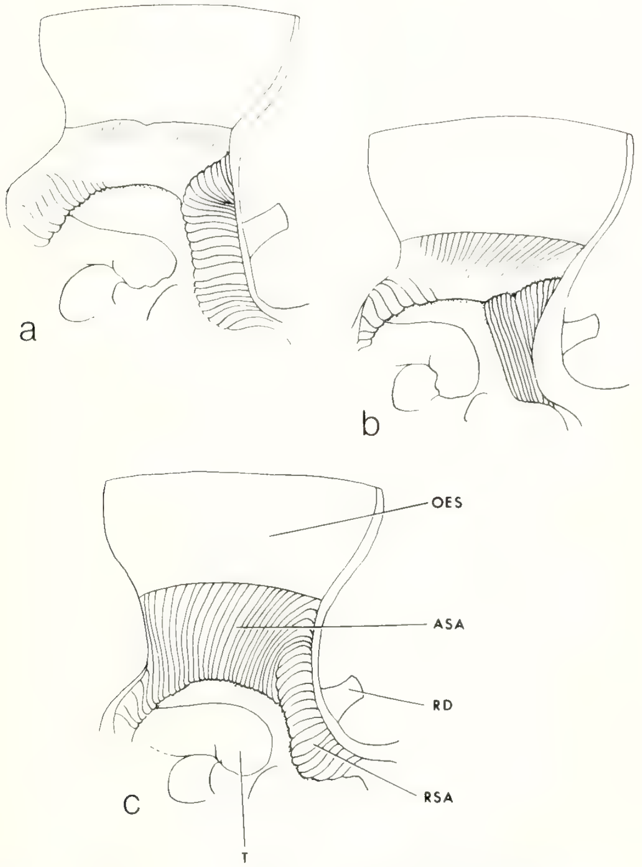

Fig. 4. Detail of the anterior and right side sorting areas of the stomach interior: a, *M. margaritifera*; b, *M. marrianae*; c, *C. monodonta*. Legend in c applies to a and b. Lines in sorting areas indicate orientation of ciliated ridges. Abbreviations: ASA = anterior sorting area, OES = esophagus, RD = right duct system, RSA = right sorting area. Horizontal field width = 7 mm.

Sorting areas were variously developed along the right side and anterior floor of the stomach interior. The right side sorting area was a low shelf (Fig. 4a), not strongly set off from the anterior stomach floor as it is in some species of the unionid genera Lampsilis (Kat, 1983b) and *Anodonta* (Smith, pers. obser.). Purchon (1958) and Dinamani (1967) did not provide sufficiently detailed descriptions of the right sorting area to make comparisons with margaritiferids. The sorting ridges of the right sorting area extended anteriorly and medially from the right side wall. A weak sorting area, analogous (but not necessarily homologous) to "SA7" of Purchon (1958), was usually present, even if barely developed. The sorting area was occasionally absent altogether (Fig. 4a).

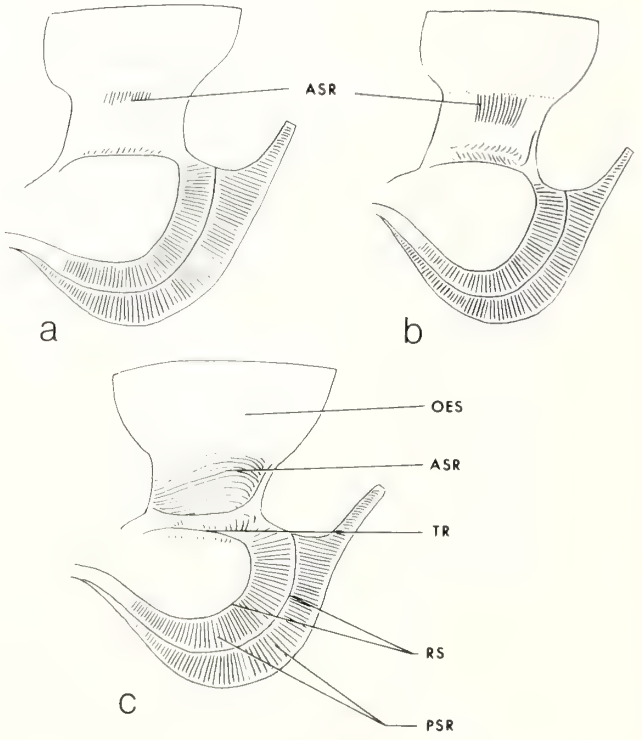

Fig. 5. Detail of the sorting areas of the stomach roof, as viewed through the roof: a, *M. margaritifera*; b, *M. marrianae;* c, *C. monodonta*. Legend in c applies to a and b. Lines in sorting areas indicate orientation of ciliated ridges. Abbreviations: ASR = anterior sorting area of roof, OES = esophagus, PSR = principal sorting areas of roof, RS = ridges delimiting principal sorting areas of roof, TR = transverse ridge. Horizontal field width = 9 mm.

The roof of the stomach contained the least developed sorting areas of all three species (Fig. 5a). The two principal posterior sorting areas (PSR, Fig. 5) of the roof were consistent with other investigated unionacean species. A poorly defined system of weak sorting ridges was sometimes present (ASR, Fig. 5a) anterior to a transverse ridge (TR, Fig. 5). The relationship of this sorting area to the anterior sorting area of the roof in *A. cygnea* ("SA8," Purchon, 1958) is unknown. These small patches of sorting ridges in *M. margaritifera* were frequently absent.

MARGARITIFERA MARRIANAE. The stomach of this species showed characteristics more typical of unionaceans than did the stomach of *M. margaritifera*. The major typhlosole was always observed to enter the opening of the left anterior duct system. The right and left anterior duct systems each opened to the stomach interior through single large openings in the stomach wall. The left posterior duct system arose from a single duct opening. The ducts leading from the opening of the left posterior system were reduced in size and complexity when compared to those of *M. margaritifera*. Anterior branches were often lacking and in a single specimen the left posterior duct system was missing altogether (Fig. 3b).

Both the anterior and right side sorting areas were developed to a greater extent than in *M. margaritifera*. The anterior sorting area was always present (Fig. 4b), if not extensively developed. Sorting ridges extended posteriorly from the esophageal rim but dissipated after a short distance. The right sorting area was considerably developed beyond the condition found in *M. margaritifera*. The area existed as a raised anteriorly lobate shelf (Fig. 4b). Sorting ridges traversed the shelf parallel to the axis of the animal. The shelf did not come into contact with the ridges of the anterior sorting area.

The morphology and position of the sorting areas (Fig. 5b) of the roof anterior was similar to that of *M. margaritifera*. The only exception noted was that the sorting ridges of the transverse ridge and the anterior sorting area were well formed and consistently present.

CUMBERLANDIA MONODONTA. Among the three margaritiferid species examined, the stomach of *C. monodonta* most closely resembled that of other unionaceans. The major typhlosole consistently entered the large opening of the left anterior duct system. The right side duct system arose from a single opening in the right wall. The left anterior duct system usually opened to the stomach through a single opening, but occasionally two openings were present, as was the case in some *M. margaritifera* specimens (Fig. 3a). The left posterior duct system commonly had a single opening in the left posterior wall. In one specimen two openings occurred. Similar to *M. marrianae*, the left posterior duct system was reduced relative to the left anterior duct system. Although anterior branches were sometimes present in the posterior duct system, they were generally very reduced.

The right side and anterior sorting areas of the stomach floor were well developed (Fig. 4c). The anterior sorting area was as complete as that reported for any other unionacean species and was joined on its right side by the well defined system of ridges of the right side sorting area. Although not strongly differentiated from the anterior sorting area, the right side sorting area was otherwise similar to that of *M. margaritifera*.

Equally well developed were the sorting areas of the roof interior (Fig. 5c). The posterior sorting areas were typical of the previous species discussed. Anteriorly, the transverse ridge increased in width as it crossed the roof from right to left and showed a well differentiated anterior border that appeared as a separate ridge. The anterior ridge was not seen in either *M. margaritifera* or *M. marrianae* (Fig. 5). Sorting ridges were prominent on the transverse ridge and, occasionally, posterior to it. A distinctive and extensive area of sorting ridges (ASR, Fig. 5c) occurred anterior to the thickened transverse ridge. Such sorting ridges coursed obliquely to the body axis and then curved sharply to the posterior on the right side.

DISCUSSION

The stomach of the Margaritiferidae, as determined from examination of three characteristic species, best conforms with the modified Type IV category of Purchon (1958) and the Section IIIC category of Dinamani (1967). Such designations are of limited use, however, as ambiquities and discrepancies in their definitions exist. This is particularly evident in attempts by Purchon (1958) and Dinamani (1967) to identify with certainty the so-called "left pouch" and correlate this feature with the various duct systems which enter the unionacean stomach. Therefore, and until a comprehensive study can provide an adequate resolution, an assignment of the descriptive term "left pouch" to any of the left wall embayments of the margaritiferid stomach has been deferred. With respect to other characteristics of the margaritiferid stomach, certain comparisons can be made with *Neotrigonia* sp. as well as other unionaceans.

A major feature which differentiates the unionacean stomach from the trigonid stomach is the alleged consistent entrance of the major typhlosole into the opening of the left anterior digestive duct system in unionaceans (Graham, 1949; Purchon, 1958; Dinamani, 1967; Smith, pers. observ.). In *Neotrigonia* sp. the major typhlosole always terminates prior to reaching the left anterior duct opening (Purchon, 1957, 1958). Also, in unionaceans a sorting area on the anterior floor of the stomach immediately posterior to the terminus of the esophagus ("SA7") is purportedly present (Purchon, 1958; Dinamani, 1967; Kat, 1983a,b; Smith, pers. obser.) whereas in *Neotrigonia* sp. it is absent (Purchon, 1957, 1958). However, in some specimens of *M. margaritifera* the major typhlosole terminates prior to the left anterior duct system opening. Furthermore, specimens of *M. margaritifera* often lack an anterior sorting area on the floor ("SA7") posterior to the esophagus. The observed variation in margaritiferid species could be merely indicative of wider variation in margaritiferids or suggestive of an intermediate condition between unionaceans and trigonids.

Relating the digestive duct systems of the examined margaritiferid species to both trigonids and other unionaceans is more difficult. The most simple form is apparently expressed by *Neotrigonia* sp. In this genus three distinct openings of the digestive duct system occur in the stomach wall, two anterior on either side of the esophageal opening and one on the left posterior wall (Purchon, 1957). The digestive duct openings of the described unionacean species vary somewhat from the trigonid condition. Both Purchon (1958) and Dinamani (1967) have described additional duct openings in the unionacean species they examined. Kat (1983a,b), other than noting the location of the two anterior duct systems, provided no specific information on the digestive duct system or the arrangement of duct openings. Therefore, unfortunately, no detailed comparisons can be made concerning the variation of duct system morphology between *Neotrigonia* sp., margaritiferids, and the many unionid species examined by Kat (1983a,b). However, based on Purchon's (1958) and Dinamani's (1967) observations, and assuming Purchon's (1957) description of *Neotrigonia* sp. is representative of the Trigonioida, the unionaceans appear to demonstrate an increase in the complexity of the digestive duct systems. This suggestion is strengthened by observations presented in this paper on the morphology and variation of the digestive duct systems in margaritiferids.

Besides the few differences between the unionaceans and the trigonids, as revealed by Purchon (1958) and the discussion above, the stomach anatomies of trigonids and unionaceans are very similar. Such strong similarity provides additional evidence for claiming a monophyletic evolution of the Unionacea and a common ancestry between the Unionacea and the Trigonioida. Such a close relationship, involving stomach and mantle anatomy and shell characteristics, has been recently expressed in a proposed revision of ordinal groups of the Pelecypoda (Nevesskaya *et al.*, 1971) in which trigonioids and unionoids are placed in a single suborder Trigoniina. It must be pointed out, however, that significant differences between the two groups in larval morphology and biology, gill morphology, and adult biology not discussed by Nevesskaya *et al.*, (1971) make unwise a reduction of the orders Unionoida and Trigonioida to a common suborder.

Using stomach anatomy to evaluate relationships between the margaritiferids and other unionacean families offers little basis for new insight. Too few unionids, hyriids, and margaritiferids have been examined or studied in detail to draw conclusions about family-specific characteristics of the various sorting and duct systems of each group. No significant differences exist in the structure of the typhlosoles or the positions of the major sorting areas. It may be that the general structure of the stomach, like other internal organs, was laid down in the most primitive ancestral unionoid and has remained essentially constant in subsequently evolved groups.

The genus *Cumberlandia*, and its relationship to the genus *Margaritifera*, has received recent attention by Davis and Fuller (1981). They concluded that the similarity of genetic distances exhibited by all margaritiferid species they examined (including *C. monodonta*) did not justify generic distinction of *Cumberlandia*. The present study provides some support for Davis and Fuller's (1981) contention. The overall morphology of the stomach of *C. monodonta* shows no greater divergence than does that of *M. marrianae* from the stomach of *M. margaritifera,* the most likely ancestor to both species (Walker, 1910). Although the anterior and roof sorting systems are most developed in *C. monodonta* (Figs. 4 and 5), there is less difference in the right side sorting area when compared to *M. marrianae* (Fig. 4). The right side sorting area of *M. marrianae* is well developed and completely unlike that of *M. margaritifera* and *C. monodonta* which have similar right side sorting areas. Furthermore, the reduction of the posterior digestive duct system in both *C. monodonta* and *M. marrianae* might be indicative of a trend in two closely related species to reduce the number of ducts communicating between the stomach and the digestive gland. Because of other yet unresolved questions regarding the anatomy of *C. monodonta*, it would be premature to reduce the genus *Cumberlandia* to a lower taxonomic category. Beyond general anatomical work, additional studies on larval morphology and biology, marsupial gill morphology (during incubation periods), and gill support structures in other margaritiferid species must be performed before further revision is justified.

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THE MUSSELS OF SOUTHWEST MISSISSIPPI STREAMS

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ABSTRACT

Bayou Pierre, Cole's Creek, Homochitto River and Buffalo River are major tributaries of the Mississippi River in southwest Mississippi. With the exception of a small portion of Bayou Pierre, all are marked by a paucity of mussels. Three years of collecting have revealed 13 species from Bayou Pierre, two from Cole's Creek, seven from Homochitto River, and none from Buffalo River. Mussels are present in these streams only in localized populations. The predominately sandy substrata appears to limit density and diversity of unionid molluscs in these rivers.

There is little published information available on the mussel fauna of southwest Mississippi streams (Bayou Pierre, Cole's Creek, Homochitto River, Buffalo River). In his monograph on Mississippi mussels, Grantham (1969) recorded a single species from the Homochitto River (*Lampsilis claibornensis* Lea, 1838) and none from the other streams. Hartfield and Cooper (1983) listed five species from Bayou Pierre (*Potamilus purpuratus* (Lamark, 1819), *Lampsilis ovata ventricosa* (Barnes, 1823), *Lampsilis straminea claibornensis* (Lea, 1838), *Leptodea fragilis* (Rafinesque, 1820), *Tritogonia verrucosa* (Rafinesque, 1820), six from the Homochitto (*Toxolasma texasensis* (Lea, 1857), *Fusconia flava* (Rafinesque, 1820), *Uniomerus declivus* (Say, 1831), *Anodonta imbecillis* Say, 1829, *Lampsilis radiata luteola* (Lamark, 1819), *Villosa lienosa* (Conrad, 1834), and commented on the rarity of mussels in this general area.

This paper is the result of a three year survey of freshwater mussels of southwest Mississippi streams. The purpose of this study was to determine the naiad species composition of these drainages as part of a statewide survey of the mussel fauna of Mississippi.

METHODS

From the spring of 1980 through the fall of 1983, a total of 148 collecting trips were made to 60 sites on southwest Mississippi streams (Fig. 1). Mussels were searched for by hand grabbing, snorkel and dipnets. Stream beds were walked and searched for dead or live specimens. Voucher specimens were deposited in the Ohio State Museum of Zoology and bivalve collection of the Mississippi Museum of Natural Science.

STUDY AREA

Southwest Mississippi streams flow across parts of three distinct physiographic regions. The western part of the study area lies in a narrow band of the Mississippi Alluvial Plain, known locally as the Delta. East of the Delta are the Loess Hills, a 30-60 km wide area of thick deposits of fine soil. Streams cut through the hills to underlying Miocene deposits of sand, gravel, and clay. Stream headwaters originate in the Pine Hills physiographic region which were formerly comprised of the red sand and gravel of the Citronelle formation. Citronelle now remains only on the highest ridges and hills and the streams flow through the underlying Miocene formations (Cross *et al.,* 1974).

Bayou Pierre (Fig. 1) drains 2770 sq. km with a mean annual flow of 33.6 cubic meters/second (cms) (Lower Mississippi Region Coor. Comm., 1974). Throughout most of its drainage the main channel consists of a shallow low-flow stream meandering within a wide sand and gravel filled eroded channel. There is no closed canopy over the stream and in many places pastures and cultivated fields extend to the banks. The river channel above Smyrna is narrow and well-defined with low banks and a few small sand and gravel bars. The channel and bank are not eroded, and throughout most of the upper reach there is a well-developed forest canopy. The upper reach also has many logjams and snags that slow flood waters and stabilize the sand and gravel substrata.

Cole's Creek drains 1088 sq. km and has a mean annual flow of 13.3 cms (Lower Mississippi Region Coor. Comm., 1974). The stream bed is wide and filled with sand and gravel throughout the drainage. At low flow Cole's

Creek is very shallow although potholes do occur around sandstone outcroppings, logs and bridges. Potholes are repeatedly filled and scoured by seasonal floods. There is little sign of channel degredation although there is some evidence of lateral erosion from the middle stretches of Cole's Creek to its mouth. Bridges on the stream are 40-50 years old and show little evidence of having supporting understructure degraded by stream movement.

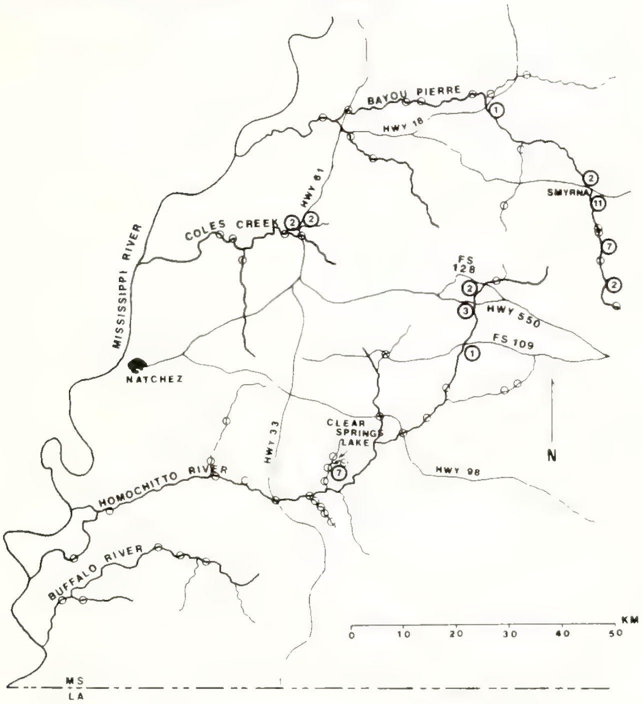

Fig. 1. Streams of southwest Mississippi. Open circles represent localities searched. Numbers represent the number of species collected at specific localities.

The Homochitto River is the largest stream in the study area and drains 3108 sq. km with a mean annual flow of 42 cms (Lower Miss. Region Coor. Comm., 1974). Headwaters and tributaries are generally canopy-covered with seasonal potholes and eddies around sandstone outcrops, logs and debris. The main channel is known for its quicksand and ever-changing channel, although most of this reputation has been earned in the last 40 years. In 1938-1940, channel modification by the U.S. Army Corps of Engineers in the lower reach of the river reduced the length by 24 km. Wilson (1979) found that the resulting increase in the slope of the water surface, resistance reduction and corresponding increase in stream velocity has caused vertical degredation of up to 5.7 meters and lateral channel movement of up to one kilometer. Tributaries in the lower reach have been similarly affected.

The Buffalo River is the smallest and the southernmost stream in the area. It drains 1087 sq. km and has a mean annual flow of 15 cms (Lower Miss. Region Coor. Comm., 1974). The middle reach and headwaters are shallow and lie within a wide sand-filled flood channel. Potholes and eddies are occasionally found along outside bends and around logs and other obstructions. In the Delta the lower reach is deep and bayou-like with little or no perceptible current.

RESULTS AND DISCUSSION

Sixteen species of unionid mussels and the Asiatic clam were collected from the study area (Table 1). All species are common Mississippi Region fauna. Live mussels were found at only 11 of the 60 sites surveyed (Fig. 1). Most of the other 49 sites provided little or no evidence of mussel fauna.

Only a few weathered shells were collected in the lower half of Bayou Pierre. Live individuals were commonly taken in the upper one third of the drainage. The largest community encountered was along a 200 m length of stream near the headwaters where eleven species were collected around sunken logs, logjams and protected eddies. At other upstream locations mussels were also found in greatest abundance around stabilized substrata protected by submerged timber. *Fusconaia flava* and *Quadrula pustulosa* (Lea, 1831) were the only species commonly collected in unprotected sand. The record of *Lampsilis straminea claibornensis* from Bayou Pierre by Hartfield and Cooper (1983) was a misidentification of *Lampsilis radiata luteola*.

Habitats in Bayou Pierre with relatively high concentrations of bivalves consisted of stable and protected sand or silty substratum in a narrow, low-flow channel defined by vegetated banks and with few sand or gravel bars. Unfortunately this type of habitat appears to be gradually disappearing from the system. Rich (1968) noted that agricultural activities and canopy removal were responsible for the gradual filling of the main channel of Bayou Pierre and that the average depth of potholes had gradually diminished from two to one meter. In his 1976 survey of the Bayou Darter, Teels stated that the eroded and non-eroded portions of Bayou Pierre met approximately 3 km downstream from the Smyrna crossing. In 1983 erosion extended to the Smyrna bridge, and it was observed during a recent visit in 1985 that the erosion extended over 1.5 km upstream from the bridge and had claimed the most diverse mussel community encountered during our survey.

No mussels were found in the main channel of Cole's Creek, but two species, *Toxolasma texasensis* and *Uniomerus tetralasmus* (Say, 1831) were collected in Shanktown Creek, a small tributary. Pools between logjams and sandstone outcrops in this narrow stream appear to maintain the mussels during low flow when there is little current.

The Homochitto is the largest stream in the study area, but only seven species have been collected from it. During 1980-1981 we were unable to find either live mussels or shells in the main channel of the Homochitto or its tributaries. However in 1982 a bivalve community consisting of *Lampsilis radiata luteola, Villosa lienosa, Toxolasma texasensis, Anodonta imbecillis, Fusconaia flava, Elliptio crassidens* (Lamark, 1819) and *Uniomerus declivus* was found in a 200 m reach between a U.S. Forest Service dam on Clear Springs Creek and Richardson Creek.

Clear Springs Dam is the oldest tributary dam in the Homochitto drainage and was dedicated the year after channelization of the lower Homochitto was completed. Substratum below the dam is sand and gravel stabilized by

Table 1. Bivalves collected in southwest Mississippi streams 1980-1983. + present, — absent.

SPECIES	BAYOU PIERRE	COLE'S CREEK	HOMOCHITTO	BUFFALO
UNIONIDAE				
Anodonta imbecillus Say, 1829	—	—	+	—
Strophitus subvexus (Conrad, 1934)	+	—	—	—
Tritogonia verrucosa (Rafinesque, 1820)	+	—	—	—
Quadrula pustulosa (Lea, 1831)	+	—	—	—
Fusconia flava (Rafinesque, 1820)	+	—	+	—
Elliptio crassidens (Lamark, 1819)	—	—	+	—
Uniomerus declivus (Say, 1831)	—	—	+	—
Uniomerus tetralasmus (Say, 1831)	—	+	—	—
Obovaria subrotunda Rafinesque, 1820)	+	—	—	—
Leptodea fragilis (Rafinesque, 1820)	+	—	—	—
Potamilus purpurata (Lamark, 1819)	+	—	—	—
Toxolasma texasensis (Lea, 1857)	+	+	+	—
Villosa lienosa (Conrad, 1834)	+	—	+	—
Lampsilis teres anodontoides (Lea, 1831)	+	—	—	—
Lampsilis ovata ventricosa (Barnes, 1823)	+	—	—	—
Lampsilis radiata luteola (Lamark, 1819)	+	—	+	—
CORBICULIDAE				
Corbicula fluminea Müller, 1774)	+	—	—	—

caddisfly nets with loose sand and detritus in pools and eddies. Above the dam the creek is shallow and the substratum is almost entirely fine sand. No mussels have been found either above the dam or in the loose sand and gravel of Richardson Creek.

Only three small communities of mussels have been found in the main channel of the Homochitto. One of these consisted of only two specimens of *Villosa lienosa* that were collected in loose sand at Forest Service (FS) Road 109. The largest collection of mussels in the main channel was at State Highway 550. *Villosa lienosa* (2), *Toxolasma texasensis* (2), and *Lampsilis radiata luteola* (1) were collected within a two square meter area on a small bed of packed sand covered by a fine layer of silt. Two specimens of *V. lienosa* and three of *T. texasensis* were collected at the FS Road 128 site after an intensive search of .4 km of stream. The record of *Lampsilis claibornensis* from the Homochitto by Grantham (1969) was almost certainly a misidentification of *Lampsilis radiata luteola,* as many specimens in this system lose their distinctive rays with age.

USGS observations from the early part of this century indicate that the main channel was deeper, narrower and more stable than its present day condition (Wilson, 1979). Although no historic records of freshwater mussels exist from this drainage, a more widespread bivalve fauna may have occurred prior to channel modifications by the Corps of Engineers.

The Buffalo River is a shallow clear-water stream in its upper and middle reach but it becomes sluggish and deep with little current when it enters the Mississippi Delta. No live mussels or shells have been found in any section of the river.

ACKNOWLEDGMENTS

Dr. David Stansbery of the Ohio State Museum of Zoology confirmed the identification of selected specimens, and Dr. Robert Jones of the Mississippi Museum of Natural Science provided helpful comments and suggestions.

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MOLLUSCAN REMAINS FROM ABORGINAL MIDDENS AT THE CLINCH RIVER BREEDER REACTOR PLANT SITE, ROANE COUNTY, TENNESSEE

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ABSTRACT

Extensive archaeological testing and excavations of multi-component aborginal sites at the proposed Clinch River Breeder Reactor Plant (CRBRP), Roane County, Tennessee were carried out from October 1973 to January 1974 and during December 1974. Approximately 23,900 valves of freshwater mussels representing at least 43 species, and about 5,000 aquatic gastropods representing a minimum of seven species were identified from the recovered shell samples. At least three species of gastropods and 26 species of naiads identified from these aboriginal habitation sites have been extirpated from this now impounded stretch of the Clinch River. Five species of naiads represented in these middens (site 40RE108) are extinct and 14 are classified as Threatened or Endangered. The prehistoric inhabitants who lived along this stretch of the Clinch River from about 800 B.C. to A.D. 1100 heavily exploited the river's molluscan resources. The archaeological samples probably accurately reflect the species composition and their relataive abundance in these early molluscan assemblages.

The rich naiad fauna of the Clinch River has been widely collected and reported. Samuel N. Rhoads, in his contributions to the zoology of Tennessee, documented the diversity of pelecypods in Tennessee and listed Patton's Ferry, Roane County, as one of his collecting locales (Pilsbry and Rhoads, 1897). Ortmann (1918), in discussing the fauna of various collecting locales on the Clinch River, noted that Rhoads collected 16 species of mussels at Patton's Ferry. Ortmann (1918) collected 28 species (including the four closely related species or forms of *Pleurobema*) from the Clinch River at Solway, Knox County, and cites Bryant Walker's collection of four species of naiads from Poplar Creek, a tributary of the Clinch River in Roane County (Ortmann, 1918). Cahn (1936) collected 45 species of naiads immediately below Norris Dam on the Clinch River at the time of the closure of the flood gates. Hickman (1937) surveyed the Clinch River in the vicinity of Norris Dam from 1935 to 1937, recording 39 species of pelecypods. These early records document some of the faunal diversity formerly found at and above the CRBRP site. Stansbery (1973) presented a preliminary report on the naiad fauna of the upper Clinch River, recording a total of 65 species and subspecies. The most recent survey of the Clinch River was undertaken by Ahlstedt (1984). At least 25 of the species in Stansbery's list (1973) are considered as either rare or endangered, while seven are probably now extinct (Stansbery, 1970, 1971; Greenwalt, 1976). Bates and Dennis (1978) provide the most recent data on naiad assemblages found in the unimpounded stretches of the Clinch River in Tennessee and Virginia.

The aquatic gastropod fauna of East Tennessee has also been extensively studied, but publications dealing with species distribution within individual river drainages are lacking except for the early work by Rhoads (Pilsbry and Rhoads, 1897) and intensive studies of *Io* spp. The genus *Io* has been carefully documented as to its clinal variations, habitat and distribution in the upper Tennessee River and its tributaries (Lewis, 1876; Adams, 1900, 1915; Lutz and Weese, 1951). Goodrich (1937; 1938) discussed the pleurocerid fauna of East Tennessee; this report was later supplemented by a reanalysis of species distribution by Sinclair (1969). Sinclair

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(1969) reported that of the seven pleurocerid gastropods formerly inhabiting the main Tennessee River, only *Pleurocera canaliculatum* (Say, 1821) was left, while the others are now found only as relic naiad populations in tributary streams. However, Isom et al. (1979) reported the rediscovery of *Lithasia verrucosa* (Rafinesque, 1820), *Lithasia geniculata salebrosa* (Conrad, 1834) and *Pleurocera alvare* (Conrad, 1834) below Wilson and Wheeler dams in northern Alabama.

Prior to impoundment and channel modification, there was a shoal area, Pickle's Shoals, located below Pickle Island at Clinch River Mile (CRM) 15.5 (24.8 km). This shoal area was recorded as being 1,200 feet (363.6 m) in length with a rock substratum and a minimum low water depth of one foot (0.3 m) (Kingman, 1900). This shoal area corresponds to the location of 40RE108.

The Clinch River Breeder Reactor Plant (CRBRP) was to be the first demonstration plant in the nation's Liquid Metal Fast Breeder Reactor program. The site chosen for its construction is situated on a peninsula formed by a meander of the Clinch River between Clinch River Mile 14.5 (23.2 km) and 18.6 (29.7 km), Roane County, Tennessee (Fig. 1). Although technically within the city limits of Oak Ridge, the site is located in the southwestern section on undeveloped property that is owned by the U.S. Government and in the custody of the Tennessee Valley Authority. Backers of this plant promoted its economic feasibility through the production of cheap and efficient energy by greater use of nuclear fuel in converting Uranium (U-238) to fissionable Plutonium (Pu-239). The 91st Congress approved initial funding of the project in 1972. Following a decade of delays, the project was stopped in 1983 when Congress denied the project further appropriations.

METHODS AND MATERIALS

In compliance with the National Historic Preservation Act of 1966 requiring survey, testing and excavation of archaeological sites in areas to be affected by federally funded construction projects, a survey of the proposed CRBRP site was undertaken and a series of freshwater shell middens was located. The site (40RE108), situated on the right bank of the Clinch River between CRM 15 (24.0 km) and CRM 15.5 (24.8 km), is about 1.5 miles (2.4 km) southeast of Tennessee Highway 58 bridge, Roane County, Tennessee (Fig. 1). Archaeological investigations at the CRBRP site were directed by Dr. Gerald F. Schroedl (1973 a,b,c; 1974; 1975), Department of Anthropology, University of Tennessee, Knoxville; these began in areas designated as I and II (Fig. 2) on 12 October 1973 and were continued until January 1974. Additional testing was carried out in area III during December 1974. Material from the excavations was waterscreened and 40-liter samples of shell were taken from each of the 2 x 2 m excavation units. In units with less than 40 liters, all of the shell was saved (Schroedl, 1973c). Approximately 500 liters of shell were returned to the Department of Anthropology, University of Tennessee, Knoxville, where all samples were carefully washed, identified, and rebagged. Most of the CRBRP shell was deposited in the Section of Zooarchaeology, Department of Anthropology, University of Tennessee; a series of voucher specimens has been placed in the collections of the Department of Malacology, Academy of Natural Sciences, Philadelphia, Pennsylvania.

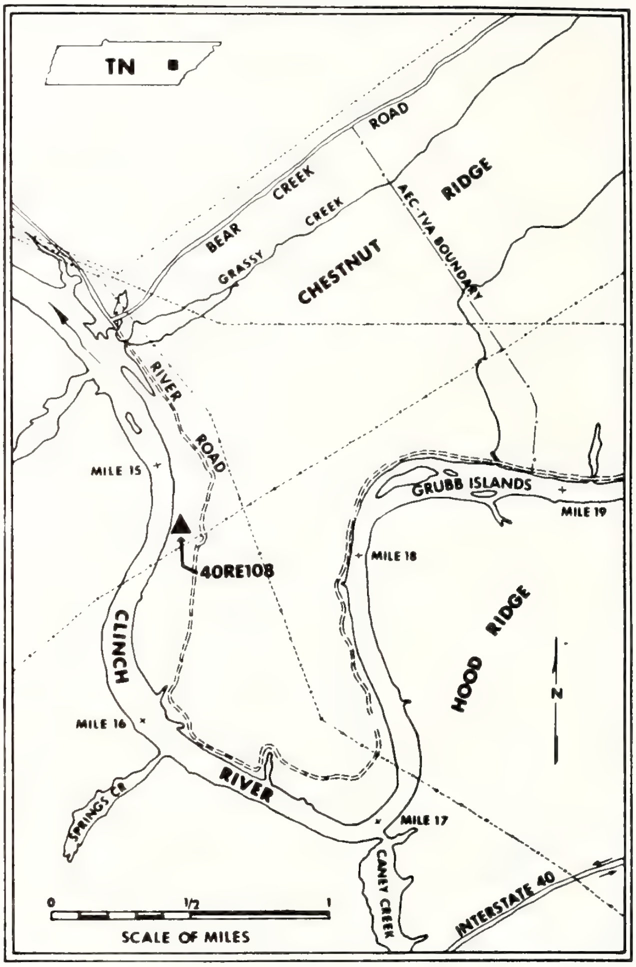

Fig. 1. Map showing location of the CRBRP site.

The site was composed of three separate shell middens that were eroding out of the river bank. Areas I and II were initially recorded by the Watts Bar Reservoir Archaeological Survey in 1941 (Nash, n.d.), while Area III was discovered during river bank reconnaissance at the time of the 1973 testing and excavations (Schroedl, 1973c). Area I was almost completely excavated; two features within this area were completely excavated and all of the recovered molluscan remains were saved. Area II was extensively sampled with about 30 to 50% of the area excavated. The Mississippian shell lense was sampled with again about 30 to 50% of the area excavated. Since these three excavation areas were being eroded by the Clinch River, it was difficult to determine the original extent of the occupation of these areas.

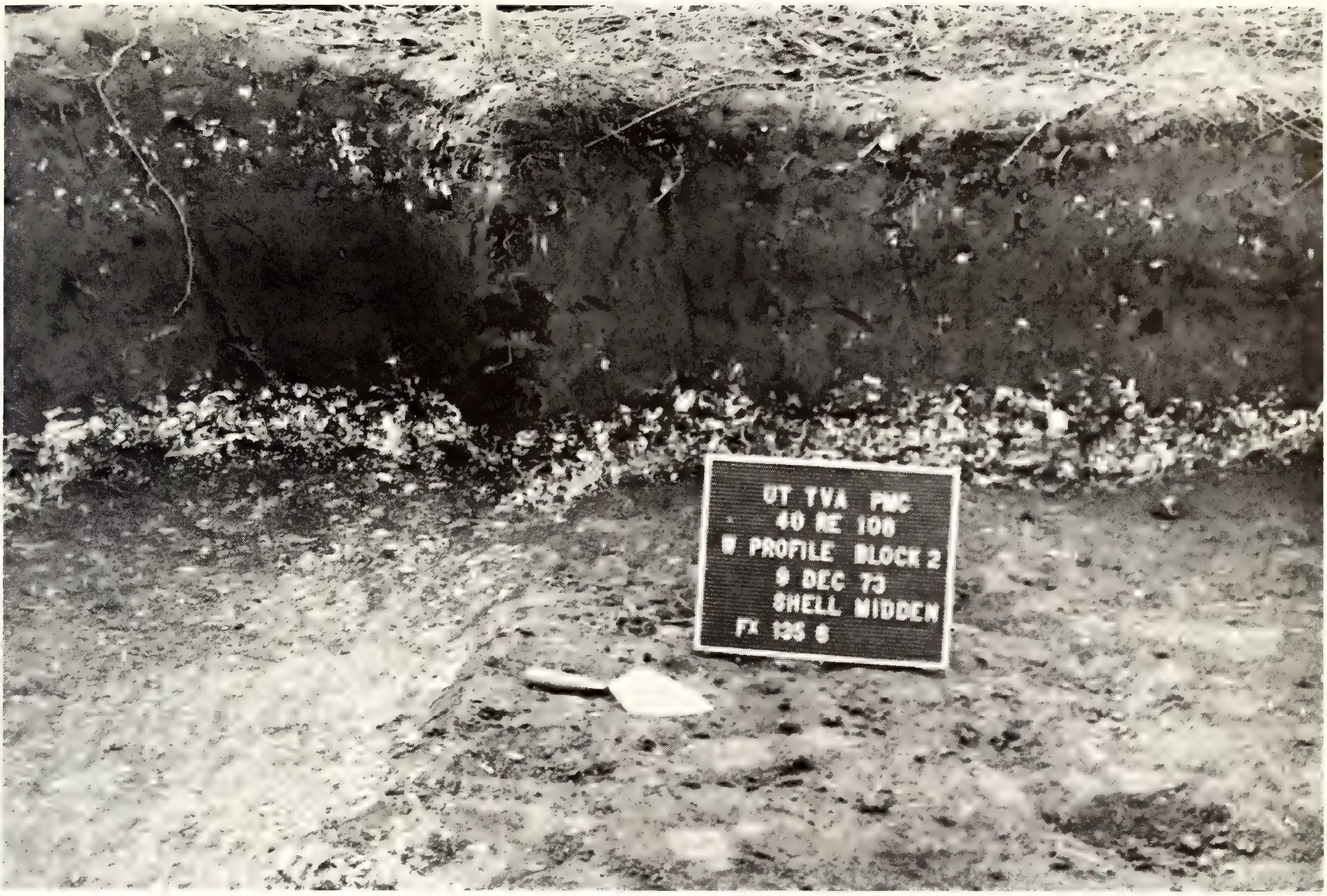

Fig. 2. One of several shell lenses exposed during 1973 excavation at the CRBRP Site.

Excavations in Area I yielded mollusks from the Plow Zone, and Middle and Early Woodland components. Area II contained mollusks in the Plow Zone and in a buried Middle Woodland component. Area III again had mollusks in the Plow Zone and in a buried Mississippian component, but it contained no Woodland materials. Two Early Woodland and three Middle Woodland radiocarbon dates were obtained (Geochron Laboratories Division, Cambridge, Massachusetts). The Early Woodland component dates between 785-345 B.C., while the Middle Woodland component dates between A.D. 65-625. The first and third dates for the Middle Woodland material were considered by Geochron Laboratories as the best of the three (Schroedl, pers. comm.). The Mississippi component is currently undated, but appears to be Early Mississippian, about A.D. 1100 (Schroedl, pers. comm.).

As used in the context of this discussion, Plow Zone refers to the humus and other soil layers disturbed by agricultural activities; Early Woodland and Middle Woodland refer to prehistoric aboriginal groups characterized by small villages or settlements whose subsistence activities depended primarily on hunting and gathering skills; and Mississippian refers to a late prehistoric cultural group who established large permanent villages and who developed agriculture (especially the growing of maize) to the extent that crops played a significant role in their food economy.

The naiads from the excavation units were intially sorted to species and recorded as to right or left valve by straum and area. The total number of valves from the three major cultural components, the Plow Zone, and areas lacking provenience are recorded in Table 1. Gastropods from each excavation unit were identified and tabulated at the same time as the pelecypods and are listed in Table 2; this table summarizes the gastropod fauna by cultrual unit. G.F. Schroedl (pers. comm.) is of the opinion that the two Middle Woodland components were contemporaneous; therefore the shell from these have been combined for comparison with the Early Woodland and Mississippian samples.

RESULTS

ACCOUNTS OF SPECIES: PELECYPODA

Amblema plicata (Say, 1817): The Three-ridge is today one of the more common and widely distributed species throughout the Tennessee River system. Valves of *A. plicata*

Table 1. Freshwater mussels identified from the CRBRP site, all components.

	Early Woodland		Middle Woodland		Mississippian		Plow Zone/No Provenience		Total: All Components/Areas	
Species	No. of Valves	%	No. of Valves	%	No. of Valves	%	No. of Valves	%	No. of Valves	%
Amblema plicata	2	2.15	375	1.85	128	4.72	18	2.09	523	2.19
Fusconaia barnesiana	2	2.15	64	.31	13	.48	1	.11	80	.33
Fusconaia subrotunda	1	1.07	1,528	7.55	155	5.71	62	7.20	1,746	7.30
Quadrula cylindrica	—	—	62	.30	38	1.40	3	.35	103	.43
Quadrula intermedia	2	2.15	261	1.29	38	1.40	2	.23	303	1.27
Quadrula metanevra	—	—	—	—	2	.07	—	—	2	.01
Quadrula pustulosa	—	—	17	.08	29	1.07	2	.23	48	.20
Quadrula sparsa	—	—	89	.44	18	.66	6	.69	113	.47
Cyclonaias tuberculata	9	9.67	1,700	8.40	278	10.24	55	6.39	2,042	8.54
Elliptio crassidens	—	—	18	.09	—	—	—	—	18	.07
Elliptio dilata	10	10.75	1,233	6.09	115	4.24	70	8.13	1,428	5.97
Lexingtonia dolabelloides	—	—	314	1.55	91	3.35	33	3.83	438	1.83
Plethobasus cicatricosus	—	—	1	T	—	—	—	—	1	T
Plethobasus cooperianus	—	—	8	.04	15	.55	1	.11	24	.10
Plethobasus cyphyus	—	—	3	.01	—	—	—	—	3	.01
Pleurobema clava	—	—	94	.46	26	.96	7	.81	127	.53
Pleurobema cordatum	—	—	12	.06	5	.18	—	—	17	.07
Pleurobema plenum	5	5.37	3,063	15.13	288	10.61	110	12.77	3,466	14.50
Pleurobema pyramidatum	3	3.22	517	2.55	95	3.50	19	2.20	634	2.65
Pleurobema spp.	4	4.30	818	4.04	176	6.48	51	5.92	1,049	4.39
Actinonaias ligamentina	20	21.50	2,822	13.94	268	9.88	118	13.70	3,228	13.50
Epioblasma arcaeformis	1	1.07	789	3.90	155	5.71	24	2.79	969	4.05
Epioblasma brevidens	4	4.30	995	4.91	48	1.77	41	4.76	1,088	4.55
Epioblasma capsaeformis	2	2.15	52	.25	24	.88	6	.69	84	.35
Epioblasma cf. *florentina*	—	—	—	—	15	.55	—	—	15	.06
Epioblasma haysiana	—	—	359	1.77	64	2.36	16	1.86	439	1.83
Epioblasma cf. *obliquata*	—	—	3	.01	—	—	—	—	3	.01
Epioblasma propinqua	1	1.07	119	.59	107	1.94	9	1.04	236	.98
Epioblasma stewardsoni	—	—	178	.88	9	.33	11	1.28	198	.83
Epioblasma torulosa	1	1.07	254	1.25	51	1.88	10	1.16	316	1.32
Epioblasma triquetra	1	1.07	20	.10	9	.33	—	—	30	.12
Lemiox rimosus	1	1.07	503	2.48	96	3.54	23	2.67	623	2.60
Lampsilis cf. *orbiculata*	—	—	1	T	—	—	—	—	1	T
Lampsilis fasciola	—	—	13	.06	5	.18	3	.35	21	.09
Lampsilis ovata	—	—	33	.16	3	.11	2	.23	38	.16
Ligumia recta	—	—	5	.02	—	—	—	—	5	.02
Obovaria cf. *subrotunda*	—	—	12	.06	3	.11	5	.58	20	.08
Villosa cf. *taeniata*	—	—	2	.01	2	.07	—	—	4	.01
Villosa trabalis	—	—	1	T	—	—	—	—	1	T
Villosa vanuxemensis	—	—	21	.10	7	.26	—	—	28	.12
Villosa sp.	—	—	4	.02	2	.07	—	—	6	.02
Cyprogenia stegaria	17	18.28	2,166	10.70	186	6.85	94	10.92	2,463	10.30
Dromus dromas	4	4.30	862	4.26	77	2.84	31	3.60	974	4.07
Ptychobranchus fasciolare	2	2.15	732	3.61	34	1.25	23	2.67	791	3.31
Ptychobranchus subtentum	1	1.07	115	.57	38	1.40	5	.58	159	.66
TOTALS	93	99.93	20,238	99.89	2,713	99.93	861	99.94	23,905	99.90

totaled 523 for all CRBRP site samples, varying between 2% and 5% for each of the three cultural components. It was present from Early Woodland through the Mississippian period, but it may not have been as numerous in prehistoric times as it is at present.

Fusconaia barnesiana (Lea, 1838): Only 80 valves of this species were identified from the sample, but this small number is not unexpected as this species tends to inhabit primarily medium-to-small rivers and headwater streams.

Fusconaia subrotunda (Lea, 1831): Nearly 1,750 valves of this species, representing slightly over 7% of all identified shells, were recovered and attest to its former

Table 2. Summary of freshwater gastropods from all components, 40RE108

	Early Woodland		Middle Woodland		Mississippian		Plowzone		Total	
Gastropoda	Total	%	Total	%	Total	%	Total	%	Total	%
Campeloma sp.	10	1.17	17	.61	5	.42	4	1.96	36	.72
cf. *Elimia* sp.	—	—	1	.03	—	—	6	2.94	7	.14
Io fluvialis	11	1.29	582	21.05	18	1.51	21	10.29	632	12.61
Leptoxis crassa	228	36.79	19	.69	451	37.83	17	8.33	715	14.27
Leptoxis cf. *praerosa*	65	7.64	7	.25	5	.42	—	—	77	1.53
Lithasia verrucosa	67	7.87	7	.25	15	1.25	—	—	89	1.77
Pleurocera canaliculatum	356	41.83	2118	76.63	698	58.55	150	73.53	3322	66.29
Unidentifiable	114	13.39	13	.47	—	—	6	2.94	133	2.65
TOTAL	851	99.98	2764	99.98	1192	99.98	204	99.99	5011	99.98

abundance in the lower Clinch River. *Fusconaia subrotunda* occurs throughout the Ohio, Cumberland, and Tennessee River systems and may be found inhabiting the deeper portions of large rivers as well as small streams and the more shallow upstream sections of rivers such as the upper Clinch and Powell. Specimens from the CRBRP samples were generally thick-shelled and inflated, thus suggesting a former habitat consisting of fairly deep water and strong current (for further information see Ortmann, 1920).

Quadrula cylindrica (Say, 1817): All of the approximately 100 valves of the Rabbit's Foot were from small (young ?) individuals; although none were complete enough for anterior-posterior length measurements, visual estimates of the fragmentary valves suggest few if any exceeded 65 mm in total length. *Quadrula cylindrica* appears to attain its greatest size in medium-to-small size streams such as French Creek, Pennsylvania and the upper Powell and Clinch rivers in extreme northeast Tennessee. The probable fast water/shoal habitat adjacent to the site area may not have been favorable for individual maximum growth and population abundance in the case of several species represented at 40RE108, those generally adapted to a smaller river or stream environment.

Quadrula intermedia (Conrad, 1836): This species was once found throughout most of the Tennessee River system above Muscle Shoals, Alabama, but due to impoundments and other detrimental factors the upper Powell and Clinch rivers contain what appears to be the last viable populations. A few (relic ?) individuals are still known to be living in the Duck River, Maury County, Tennessee (S. A. Ahlstedt, pers. comm.). Although apparently not numerous in the lower Clinch River, *Q. intermedia* appears to have been well established; like *Q. cylindrica*, all valves of this species were small and compressed with none having developed the thick shell or large size of those now inhabiting the upper Powell River.

Quadrula metanevra (Rafinesque, 1820): The *Quadrula metanevra*-*Quadrula sparsa* complex poses a taxonomic problem that is not easily resolved. Superficially *Q. sparsa* resembles *Q. metanevra* in general shape of the shell, but is more compressed and lacks the large, distinct, protruding tubercles forming the high posterior ridge characteristic of typical *Q. metanevra*. The majority of CRBRP site specimens exhibit a more uniform distribution and size of tubercles over the posterior two-thirds of the valve; some possess a distinct sulcus that is nearly or completely void of tubercles (as in typical *Q. sparsa*) while others lack the sulcus and distinct posterior ridge and show a more uniform distribution of tubercles (Fig. 3). These specimens appear to be a down river form of *Q. sparsa*, yet in some specimens characters appear similar to those defined by Morrison (1942) for a new species, *Quadrula biangulata* (Morrison, 1942), he described from the Pickwick Basin mounds. Whatever the identity of the organism, it was not overly abundant (113 valves) in the sample and comprised only 0.5% of all naiads recovered. Only one small individual (paired valves) of typical *Q. metanevra*, a species previously unreported from the Clinch River, was encountered in the CRBRP site naiad sample (Mississippian component).

Quadrula pustulosa (Lea, 1831): Today the Pimpleback is one of the most widely distributed and common species of mussels found in Tennessee, occurring in small streams as well as in large rivers. Apparently it was not a common shell in the Tennessee River system in aboriginal times. Only 48 valves of *Q. pustulosa* (0.20% of total) were identified from the CRBRP site sample; it was also rare or absent in shell midden samples examined from several other sites along the Tennessee River in Rhea and Meigs counties (Parmalee et al., 1982).

Cyclonaias tuberculata (Rafinesque, 1820): Shells of the Purple Warty-back were second in number (2,042) only to those of *Actinonaias ligamentina* (Lamarck, 1819). Morrison (1942:357) reported *C. tuberculata* as being ". . . extremely abundant in all the mounds" in the Pickwick Basin shell mound samples, while it was less than abundant but still common in the naiad material analyzed from the Widows Creek Site (Tennessee River) in northeast Alabama (Warren 1975). Although this species has been greatly reduced in numbers or completely eliminated in impounded areas, it still occurs commonly in numerous streams and rivers such as the upper Clinch and Powell. It was apparently common in the shoals area adjacent to the CRBRP site and the Indian made good use of this mussel; all age sizes were represented in the samples, from juveniles the size of a quarter to extremely large, old individuals. Valves of *C. tuberculata* varied from about 8% in the Middle Woodland component to 10% in the Mississippian.

Elliptio crassidens (Lamarck, 1819): Considering the present abundance of the Elephant Ear in the Tennessee River and its major tributaries, even in stretches affected by impoundment, it is surprising that only 18 valves were recovered. Morrison (1942) reported only a few individuals from the Pickwick Basin mounds and attributed its rarity to the fact that it inhabits water too deep for wading. Although this is generally true, it almost certainly could have been taken in considerable numbers—if present—during periods of low water.

Elliptio dilatata (Rafinesque, 1820): The Spike is one of the most common mussels found throughout the Tennessee River system, occurring in headwater streams as well as in the large, deep water rivers. The 1,428 valves of *E. dilatata* comprised 6% of all identified naiad remains recovered at the CRBRP site. Although numerous shells of small juveniles were recovered, thick heavy valves of old adults—indicative of a large river/fast current habitat—were also common.

Lexingtonia dolabelloides (Lea, 1840): A total of 438 valves, which comprised 2% of all mussel shells recovered, were determined to be this species. The shell of *L. dolabelloides* exhibits considerable variation in size, shape, and degree of inflation and certain individuals superficially resemble forms of *Pleurobema* to which *L. dolabelloides* is closely related. Weathered specimens from an archaeological context compound the problem. Many of the "less-than-typical" valves of the *Pleurobema/Lexingtonia* complex from the CRBRP site were difficult to identify with complete certainty. *L. dolabelloides* seems to reach its greatest abundance in medium-sized rivers (e.g. the Duck River in Middle Tennessee), although former shoals of the Tennessee River apparently supported large populations.

Plethobasus cooperianus (Lea, 1834): Today the Orange-footed Pimple-back is rare and may be on the verge of extinction. In Tennessee it formerly inhabited the larger rivers such as the Tennessee, French Broad and Holston; Ortmann (1918) reported it as also occurring in the lower Clinch. There are apparently no records of its former abundance but, judging by the paucity of specimens (about 17 individuals) from the CRBRP site samples, it was not common in the lower Clinch River during aboriginal times. In archaeological context shells of *P. cooperianus* might be confused with those of *Cyclonaias tuberculata*; fresh specimens differ from the latter species in having white rather than purple nacre and a much shallower beak cavity. *Plethobasus cooperianus* is *Plethobasus striatus* (Rafinesque, 1820) as used by Bogan and Parmalee (1983). The type of *P. striatus* as preserved in the Academy of Natural Sciences, Philadelphia, Malacology Collections, is *Obovaria subrotunda* (Rafinesque, 1820), while the type in the Museum National d'Histoire Naturelle, Paris, France is *Cyprogenia stegaria*. Thus, we consider *P. cooperianus* the valid name for the species.

Plethobasus cyphyus (Rafinesque, 1820): The Sheepnose was poorly represented in the CRBRP site samples (3 specimens), although it is a common shell in the upper Clinch and Powell rivers today. The typical form of *Plethobasus cyphyus* was apparently extremely rare in the lower Clinch in prehistoric times.

Plethobasus cicatricosus (Say, 1829): Some authors (e.g. Burch, 1975) consider this species synonymous with *P. cyphyus*, but one specimen recovered from the CRBRP site Middle Woodland component and the numerous valves encountered in Woodland and Dallas (Mississippian) shell middens along the Tennessee River in Meigs and Rhea counties (Parmalee *et al.*, 1982) are quite distinct from the modern shell form of *P. cyphyus*. Valves of *Plethobasus* from these latter sites are oblong, compressed and thick, the beaks project forward and there is a row of low, dense tubercles runnig from the beak to the center of the ventral margin. Whatever form or species these valves represent, it was apparently rare in the lower Clinch.

Pleurobema clava (Lamarck, 1819): In the Interior Basin drainage, *P. clava* occurs in the Ohio, Cumberland, and Tennessee River systems. Valves assigned to this species from the CRBRP site were typical of medium-to-large river forms in that the anterior portion of the shell was thick and swollen and the beaks were more anteriorly positioned. Another species, *Pleurobema oviforme* (Conrad, 1834), is closely related to and possibly a southern counterpart of *P. clava* which occurs most often in small-to-medium sized rivers. However, no valves could be assigned to *P. oviforme* and it is felt that identification of the 127 specimens as *P. clava* is correct.

Pleurobema cordatum Rafinesque, 1820 (= ?*Pleurobema obliqum* [Lamarck, 1819]), *Pleurobema coccineum* (Conrad, 1836), *Pleurobema plenum* (Lea, 1840), and *Pleurobema rubrum* (Rafinesque, 1820) (= *P. pyramidatum*): The taxonomic problems involving the correct assignment of *P. plenum, P. rubrum* and *P. coccineum* to subspecific or species rank has already been considered. Athough *P. coccineum* occasionally is found inhabiting large rivers, it apparently attains maximum abundance in smaller streams and headwaters; no valves of the *Pleurobema* spp. group from the CRBRP site could positively be assigned to this form. Neel and Allen (1964) comment that *Pleurobema cordatum pyramidatum* ". . . occurred only on the big [Cumberland] river bars," and that *Pleurobema cordatum plenum* ". . . was found in goodly numbers on all main stem bars," and that these variants or subspecies ". . .often occur side by side with the parent form [*P. cordatum*] . . . seemingly have the same habitat preferences as the parent form." Judging from the various forms of *Pleurobema* represented in the CRBRP site material, the same situation must have formerly prevailed in the lower Clinch River in the vicinity of this site.

Shells of the parent form were few in number; however, considering all valves of the *Pleurobema cordatum* complex together, they totaled 5,166 which constituted nearly 22% of the entire sample. Valves of *P. plenum* alone comprised almost 15% of the total sample. The shoals and gravel bars

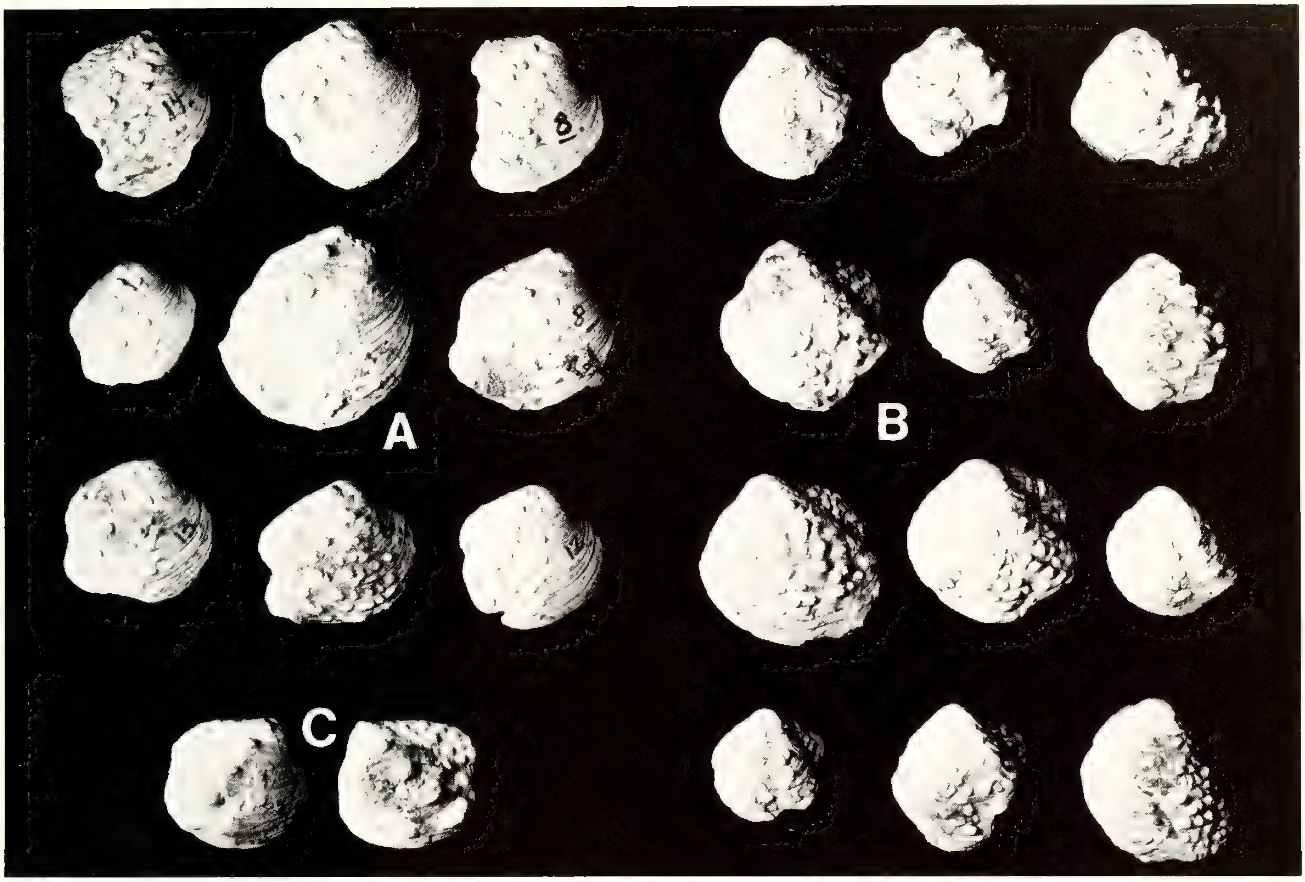

Fig. 3. Examples of right (A.) and left (B.) valves of *Quadrula sparsa* from the CRBRP Site illustrating variation in pustule arrangement. The specimens of *Quadrula metanevra* (C.) encountered in the CRBRP site molluscan sample.

adjacent to the site must have supported a rich and varied naiad fauna with individuals of the *Pleurobema* group and those of the following species comprising about one third of the population.

Actinonaias ligamentina (Lamarck, 1819): Slightly over 3,200 shells of the common Mucket were identified, the largest number for any single species recorded from the CRBRP site. Nearly 1,700 individuals were represented and their shells comprised 13.5% of all valves recovered. Today the Mucket is still one of the most common naiads in the unimpounded Clinch River above the Norris Reservoir. During the various periods this site was occupied, *A. ligamentina* must also have occurred abundantly in the shoal areas of the lower Clinch River. Because of the close similiarity in shell characters between this species and the Pink Mucket (*Lampsilis orbiculata* (Hildreth, 1828)), especially in the males, a few of the valves recorded as *A. ligamentina* may be those of the Pink Mucket.

Epioblasma arcaeformis (Lea, 1831): The Sugar Spoon was once widespread throughout the Tennessee and Cumberland River systems, but it has not been collected in over 50 years and is presumed extinct (Stansbery, 1970). In addition to inhabiting small tributary streams, it occurred on shoals of the larger rivers such as the Tennessee and lower Clinch. Over 900 valves of *E. arcaeformis* were recovered in the CRBRP site samples with both juveniles and old adults being represented. All species of *Epioblasma* identified from the site are relatively small mussels. However, as in the case of nearly all species represented in the samples, small juveniles as well as large adults were collected, so it would appear that the Indian was not selective as to the size of individuals (or species) utilized.

Epioblasma brevidens (Lea, 1831): Of the 10 species and/or forms of *Epioblasma* represented in the CRBRP site samples, valves of *E. brevidens* were the most numerous (1,088). This mussel is still common locally in the upper Clinch and Powell rivers but, like many of the smaller species formerly found in shoal and bar areas of big rivers, it has disappeared in the impounded stretches. Shells of all species of *Epioblasma* identified from the site numbered nearly 3,400 and comprised 14% of the total.

Epioblasma capsaeformis (Lea, 1834): Ortmann (1925) stated that this species is ". . . apparently as abundant in the lower Tennessee drainage as in the upper, both in larger and smaller streams." It apparently was not numerous in the shoal area adjacent to the site as only 84 valves were recovered. Identification of several of these closely related forms is difficult, and often impossible, when the valves are chalky and incomplete. This species and *Epioblasma florentina* (Lea, 1857) are very similar, and the problem of distinguishing between the two from archaeological specimens usually cannot be done with absolute certainty. Only 15 shells of *E.* cf. *florentina* were identified from the sample.

Epioblasma haysiana (Lea, 1833): Once found widely distributed throughout the upper Tennessee and Cumberland River drainages in both large rivers and small tributary streams, *E. haysiana*, the Acorn, was reduced to a single population in a 10 mile (16.0 km) stretch of the upper Clinch River in Virginia (Stansbery 1970). In all probability it is now extinct, judging by the present poor condition of that section of the river and the failure to find a single shell during recent collecting trips. A total of 439 valves were recovered, suggesting that it was probably only moderately common in the lower Clinch River in prehistoric times.

Epioblasma stewardsoni (Lea, 1852): Differences between archaeological specimens of this species, *Epioblasma lewisi* (Walker, 1910) and *Epioblasma flexuosa* (Rafinesque, 1820) are often subtle; added to the problem of incomplete preservation are the normal variations between and among species due to age and sex. Therefore, it is possible that a few of the 198 specimens recorded in Table 1 as *E. stewardsoni* are *E. lewisi* and/or *E. flexuosa* but, for the most part, all compared closely with *E. stewardsoni*. All three species are now extinct; *E. stewardsoni* inhabited the Tennessee River and apparently the lower stretches of its major tributaries, while *E. lewisi* (a small river form of *E. flexuosa*?: Johnson, 1978) occurred in the upper Tennessee, Clinch and Holston rivers.

Epioblasma cf. obliquata (Rafinesque, 1820) [= *Epioblasma sulcata* (Lea, 1824)]: This is an Ohio River drainage species with the form *Epioblasma obliquata sulcata* occurring in the Green River, Kentucky and in the Cumberland River, Kentucky/Tennessee. Although the three specimens from the Middle Woodland component compared closely with fresh material of *E. obliquata*, our determinations are only tentative in light of the past distribution of this species and the fact that these mature specimens may represent males of *Epioblasma propinqua* (Lea, 1857).

Epioblasma torulosa (Rafinesque, 1820), **Epioblasma propinqua** (Lea, 1857): Two distinct forms (or species if *propinqua* should be treated as such) of the *E. torulosa* complex were apparent in the CRBRP site material. The species *Epioblasma torulosa gubernaculum* (Reeve, 1865) appears to inhabit medium-sized rivers while *E. propinqua*, which has not been collected in over 50 years and is presumed extinct, reached its greatest population density in the Tennessee River and the lower reaches of its major tributaries. Although the majority of shells of *E. torulosa* from the CRBRP site could be separated into either *E. t. gubernaculum* (valves compressed, tuberculate) or *E. propinqua* (valves inflated, heavy, and lacking tubercules), a few appeared to be intergrades between the two. Regardless, both species occurred in the shoals and riffles adjacent to the site; combined, valves of *E. torulosa* and *E. propinqua* totaled 552 which comprised slightly over 2% of the total.

Epioblasma triquetra (Rafinesque, 1820): Although the Snuffbox is an inhabitant of both large and small rivers, it tends to be most numerous in the small-to-medium sized rivers. It is, for example, a common shell in the upper Clinch and Powell rivers; judging by the paucity of valves (30) from the CRBRP site samples, it must have been uncommon to rare in that stretch of the lower Clinch.

Lemiox rimosus (Rafinesque, 1820) [= *Conradilla caelata* (Conrad, 1834)]: This small species was once widespread in the Tennessee River system, but populations now appear localized in a few rivers such as the Duck and the upper Clinch and Powell. Ortmann (1918) reported it from the lower Clinch River but commented that, although of wide distribution, it was found nowhere in great numbers. Over 600 valves of *L. rimosus* were identified, suggesting that it may have been a moderately abundant shell at the site location. Living specimens are not easy to find because of their habit of remaining nearly or completely buried in the substrate.

Lampsilis ovata (Say, 1817): The Pocketbook is one of the most widespread and locally common mussels occurring throughout the unimpounded river systems in Tennessee. It is a large species and the valves vary in thickness from moderately heavy to extremely thick. Since most of the specimens identified from the CRBRP site samples consisted of only the umbo/tooth/hinge line, it is possible that preservation, or the lack of it, was a factor in the paucity of valves (38) recovered. However, had *L. ovata* been a common species in the lower Clinch at the CRBRP site, it probably would have been collected by the Indian as one of the more desirable large forms and it would, therefore, have been better represented in the samples.

Lampsilis fasciola (Rafinesque, 1820): Ortmann (1925) stated this species is "... of very general distribution in the Ohio drainage, in the Cumberland, lower and upper Tennessee systems, but somewhat scarce in larger rivers, more abundant in smaller ones." Only 21 valves of *L. fasciola* were recovered, so it is apparently true that this species was also rare in the large rivers, at least the lower Clinch, in prehistoric times.

Lampsilis orbiculata (Hildreth, 1828): This large river species of *Lampsilis* has a wide distribution in the major river systems of the Interior Basin, including the Tennessee and Cumberland. Except for the impounded stretches of the middle Cumberland River where it has been taken in considerable numbers by commercial shellers (Parmalee et al., 1980), the Pink Mucket is an uncommon shell throughout most of its range. Only one valve (female) from the site was determined with a degree of certainty as being *L. orbiculata*.

Ligumia recta (Lamarck, 1819): The Black Sandshell is another widely distributed species throughout the major river drainages of the Interior Basin, inhabiting both large and small rivers. It is not a rare species, but it never reaches a population density comparable to that of *Actinonaias ligamentina*, even under ideal habitat conditions. It must have been a rare shell in the lower Clinch at the CRBRP site as only five valves of *L. recta* were encountered in the samples.

Obovaria subrotunda (Rafinesque, 1820): Although this widespread species inhabits both large and small rivers, remaining Tennessee populations occur in medium-to-small sized rivers such as the Duck and Red. It was perhaps never common in the lower Clinch River; only 20 specimens were encountered in the samples.

Villosa taeniata (Conrad, 1834): This is a species usually restricted to medium-sized to small rivers (e.g. tributaries of the Stones River; Red River; upper Powell River), so the recovery of only four valves tentatively identified as *V. taeniata* from the CRBRP site is not surprising.

Villosa vanuxemensis (Lea, 1838): *V. vanuxemensis* is a locally common member of the naiad fauna of the upper Cumberland and Tennessee River drainages and it is usually found inhabiting only the medium-sized rivers and smaller tributary stream. ***Villosa trabilis*** (Conrad, 1834), of which only one valve was recovered at the CRBRP site, occupies a similar aquatic habitat. Species belonging to this genus are not surprisingly poorly represented in these middens from the lower Clinch River.

Cyprogenia stegaria (Rafinesque, 1820) [= *Cyprogenia irrorata* (Lea, 1830)]: The Fan Shell was once widely distributed and common in the Ohio, Cumberland, and Tennessee River systems, but its former range and populations have been greatly reduced. The last remaining viable population in Tennessee today appears to be restricted to the upper Clinch River. Nearly 2,500 shells of *C. stegaria* (about 10% of the total) occurred in the CRBRP site samples, attesting to its former abundance in the shoal areas of the lower Clinch. Morrison (1942) found it moderately abundant in all of the Pickwick Basin mounds.

Dromus dromas (Lea, 1834): Like *C. stegaria, D. dromas* was an abundant shell throughout the Tennessee and Cumberland River systems but it, too, has been eliminated from most of its former habitat. Its prehistoric abundance in the Tennessee River is exemplified by the approximately 14,100 valves (22% of individuals) recovered at the Widows Creek site (Warren, 1975) and by about 9,800 valves (45% of all naiad shells) reported from 14 Woodland and Mississippian middens in the Chickamauga Reservoir, Tennessee River (Parmalee et al., 1982). Morrison (1942), in commenting on the Pickwick Basin mound material, stated that it was "One of the most abundant species in these shell deposits. According to the number of specimens handled in the course of this study, *dromas* must have been very abundant here previously. These specimens are of good size for the species, and made up a major part of the total mussel fauna gathered for food." Similarly, *D. dromas* must have been a comon species in the lower Clinch River, although perhaps not as abundant as it was in the Tennessee. Nevertheless, nearly 1,000 valves, about 4% of the total, were recovered in the CRBRP site middens; this mussel, because of its large size and abundance, was probably one of the more important food species.

Ptychobranchus fasciolare (Rafinesque, 1820): Valves of the Kidney-shell totaled nearly 800, representing about 3% of all identified naiads. Ortmann (1918) commented that it is ". . . widely and uniformly distributed over the upper Tennessee region, but nowhere in great numbers." It was apparently moderately common in the shoals and gravel bars adjacent to the site, but has now disappeared from the lower Clinch, like most species adapted to such a habitat, due probably to river impoundment.

Ptychobranchus subtentum (Say, 1825): An inhabitant of the upper Tennessee and Cumberland River systems, *P. subtentum* is ". . . more abundant toward the headwaters, and rather rare in the big rivers" (Ortmann, 1918). A total of 159 valves of this species was identified from the CRBRP site samples, thus establishing the former presence of a population at this point in the lower Clinch but one that was probably not extensive.

GASTROPODA

The excavations in Areas I, II, and III yielded 5,011 shells of freshwater gastropods, representing seven species, which were found mixed with the valves of pelecypods (Table 2). The following discussion provides an evaluation of the probable taxonomic position of the gastropods from the CRBRP site, former habitat requirements, and their importance in the subsistence of the inhabitants.

Campeloma indeterminate species: This group was left at the generic level due to the present confusion existing over the synonymy of the multitude of named species and forms. Rhoads collected *Campeloma ponderosum* (Cooper, 1834) from the Clinch River below Patton's Ferry, Roane County (Pilsbry and Rhoads, 1897). Hickman (1937) lists only one species of *Campeloma* from the Clinch River, *Campeloma rufum* (Haldeman, 1841), which was found in abundance in the vicinity of Norris Dam. Bickle (1968) lists four species of *Campeloma* as occurring in Tennessee: *Campeloma crassula* (Rafinesque, 1819), *Campeloma decisum* (Say, 1816), *Campeloma exile* (Anthony, 1860), and *Campeloma geniculum* (Conrad, 1834). Clench (1962) lists *C. ponderosum* as a synonym of *C. crassula, C. rufum* is apparently synonomous with *C. geniculum,* and Baker (1902) and Binney (1865) saw *C. geniculum* as a synonym of *C. decisum.* Burch (1982) lists *C. crassula* and *C. decisum* from Tennessee. In consideration of these views, the archaeological specimens of *Campeloma* might be referred to *C. crassula,* based on the collection records of Rhoads (Pilsbry and Rhoads, 1897) or *C. decisum* based on Hickman's collecting of *C. rufum* in the lower stretches of the Clinch River (Hickman, 1937). Morrison (1942) noted that *Campeloma* spp. would have been available to the prehistoric Indians in quantity since it occurs in shallow areas close to shore.

Elimia sp: Only seven gastropods were encountered that could be referred to this genus; the species was not determined.

Io fluvialis (Say, 1825): This gastropod was formerly widespread in the Tennessee River and its tributaries in East Tennessee (Adams, 1900, 1915), but it is now restricted to the upper Clinch, Powell and Nolichucky rivers above impoundment. Adams (1915) noted that the specimens of *Io fluvialis* he collected from the lower Clinch River were very spinose, but did not assign a subspecies or form name to the specimens. The archaeological specimens from the CRBRP site ranged from about 2 cm in length to very large, slender, spinose individuals measuring 6.5 cm in length. *Io fluvialis* is typically found in riffle areas with good current and often occurs in association with *Leptoxis* spp., *Lithasia* spp., and *Pleurocera* spp. (Lewis, 1876; Adams, 1915; Hickman, 1937).

Leptoxis (Athearnia) crassa (Haldeman, 1841): Bogan and Parmalee (1983) and Burch (1982) provided the taxonomic history of this species. We will use Burch's generic placement based on radular characters. Hickman (1937) reported *Leptoxis crassa anthonyi* (Redfield, 1854) (= *Eurycaelon anthonyi*) and *Lithasia geniculata* (Haldeman, 1840) from the Clinch River below Norris Dam. However, her figures of *L. geniculata* appear to show *L. crassa* and the figure of *L. c. anthonyi* appears to be *Leptoxis praerosa* (Say, 1824). She reported that *anthonyi* was found on rocks in knee deep water with *Leptoxis* (= *Anculosa*) and *Io (Hickman, 1937). This species was common in the CRBRP archaeological samples (Table 2).*

Leptoxis cf. ***praerosa***: Most of the 77 specimens of *Leptoxis* compared well with *L. praerosa*; however, a few of the smaller specimens appear intermediate between *L. praerosa* and *Leptoxis subglobosa* (Say, 1825) (See Walker, 1908).

Lithasia verrucosa (Rafinesque, 1820): The majority of these specimens occurred in the Early Woodland component. Morris (1939) notes that *L. verrucosa* is generally found in bends of sluggish streams, half buried in mud and decaying vegetation. They have been collected by the authors on rocks in shallow water with little current immediately adjacent to the river's edge in the Nolichucky River, East Tennessee.

Pleurocera canaliculatum:Goodrich (1937) collected *Pleurocera canaliculatum undulatum* (Say, 1829) from the Clinch River in Roane and Anderson counties. However, no attempt was made to identify the forms represented at the CRBRP site. This was the most common gastropod identified in the pelecypod sample (3,322 individuals). Goodrich (1938) lists the habitat of *P. canaliculatum* as generally muddy situations; Morris (1939) commented that this species is often found on the open unvegetated shore in moderately shallow water, sometimes buried in the mud with only the spire protruding. *Pleurocera* would have been locally available along with *Campeloma* and *Lithasia*.

These gastropods were all common prior to impoundment and modification of the rivers. *Io fluvialis, Leptoxis praerosa,* and *Lithasia verrucosa* are living only as isolated, relic populations and have been listed as Rare and Endangered (Sinclair, 1969; Stansbery, 1970, 1971; Stein, 1976). Sinclair (1969) found that of the formerly diverse gastropod fauna of the Tennessee River, only *Pleurocera canaliculatum* remained in sizable numbers. The current population status of *Campeloma* spp. is unknown, but it is not endangered due to its generalized habitat requirements and wide distribution.

Cf. ***Busycon*** sp.: One fragment of the body whorl of a marine conch was recovered in Feature 7, a Middle Woodland feature in Area I. This marine shell would have been transported to Tennessee from either the Gulf of Mexico or the southeastern Atlantic Coast. Drilled marine conch columella were found in a Hamilton Late Woodland burial mound (40RE124) adjacent to 40RE108 (Cole, 1975). Marine shells were also recovered in two Early Woodland sites in East Tennessee, the Camp Creek and the Rankin sites (Lewis and Kneberg, 1957; Smith and Hodges, 1968).

DISCUSSION AND CONCLUSIONS

Problems involving the taxonomy of freshwater bivalves have been prevalent for the past century and many have yet to be resolved. Since most genera and species descriptions are based on soft parts, the zooarchaeologist is at a disadvantage in making specific determinations because only isolated valves from the archaeological context are available. Often these shells are chalky and incomplete and any diagnostic color or pattern in the periostracum fades or is obliterated after the specimen has been buried for some time. It is true that the shell structure of many species such as *Amblema plicata* (Say, 1817), *Cyclonaias tuberculata* (Rafinesque, 1820), *Quadrula cylindrica* (Say, 1817), *Lemiox rimosus* (Rafinesque, 1820), and *Cyprogenia stegaria* (Rafinesque, 1820) consists of diagnostic ridges, plications, tubercles and the like which are generally easily recognizable regardless of the loss of color or pattern. It is also true that the often subtle differences in shell color, design pattern and/or structure of fresh specimens used to distinguish or separate certain other closely related species have limited value when it comes to identifying archaeological specimens.

Another problem that must be considered in certain instances when attempting to arrive at specific identifications is that of determining whether or not the specimen or specimens are actually "good species" or instead subspecies, ecological forms, or variants that reflect former habitat conditions. To illustrate, some researchers recognize three distinct large river species, *Pleurobema plenum, Pleurobema coccineum,* and *Pleurobema rubrum,* that are considered by others to be subspecies or forms of *Pleurobema cordatum.* Neel and Allen (1964) provide informative comments on this complex from the Cumberland River Basin; they treated their specimens of *Pleurobema* as subspecies, but commented that "The trinomial system is a convenience, and this complex has long been a part of our mussel lore, but no claims are made for the validity of the subspecific rank." This problem was inherent in several species or forms represented in the CRBRP site samples (e.g. the *Pleurobema cordatum* complex and certain closely related species of *Quadrula, Epioblasma,* and *Villosa*).

The vast quantities of pelecypods that comprise the major portion of the faunal debris of "shell mounds" and midden deposits along the large rivers in the Midwest and Middle South have long been of special interest to both the archaeologist and zoologist. Because these huge concentrations often consist almost entirely of shells, especially sites of primarily Archaic and/or Woodland components, it was generally held that mollusks must have provided the basic meat resource in the subsistence of these early prehistoric peoples. However, at least one study (Parmalee and Klippel,

1974) has shown that the nutritional value of the freshwater mussel is minimal and that, in light of all potential food resources available to the Indian, mollusks provided only a supplemental food source in the diet. Bennett (1955) provides an interesting quote from a 1634 narratiave by Wood on the apparent disdain for mollusks by Indians of southeastern New England:

> "They keepe no set meales, their store being spent, they champe on the bit, till they meete with fresh supplies, either from their own endeavours, or their wives industry, who trudge to the Clambankes when all other means faile . . ."

Nevertheless, naiads as well as certain aquatic gastropods were utilized extensively and, in the southern latitudes, comprised an almost limitless food resource that was available throughout most if not all seasons. Barnes (1823), commenting on the appearance of unionids, remarked that "Not only is the appearance of the shells different to the eye of the naturalist, but also the taste of the included animals, to the palate of the epicure." Hildreth (1828), in discussing the naiades in the vicinity of Marietta, Ohio, observed

> "Their beauties were not unknown, or neglected by that ancient race of men who once inhabited the pleasant vales of Ohio; as the valves of some of the most interesting kinds are often found buried in mounds, intermixed with other articles considered as valuable by the builders of those venerable monuments of the dead. They must also have been deemed very valuable as an article of food; as we find vast beds of the calcined shells, in the banks of the river, usually several feet below the present surface, and near them a hearth of stone with ashes and fragments of deer and fish bones promiscuously interspersed. In those seasons of the year, when the waters were low, and game scarce, they no doubt constituted a large portion of their food. Some of the species are very fine eating, and much admired by the lovers of shell fish at the present day, particularly the Unio ellipticus and Alasmodonta complanata, which are very large, and in the month of September abound in fat, to the extent of one or two ounces of clear oil in a single individual."

Matteson (1958, 1960) has shown that it may be possible to reconstruct past aquatic environments from the analysis of mollusks recovered in Indian shell heaps and middens. The known habitat requirements of aquatic species represented in such aborginal deposits serve as an index of the former river conditions from which they were collected. Thus far studies dealing with mollusks from archaeological sites in Tennessee have been few in number (see Warren, 1975; Parmalee *et al.*, 1980, 1982). The identification and analysis of over 100,000 naiad and gastropod (aquatic and terrestrial) shells from the shell mounds of the Pickwick Landing Basin in the Tennessee River Valley by Morrison (1942) was one of the earliest and most detailed studies of aboriginal shell deposits from the Southeast. As additional sites, such as CRBRP, are excavated and their faunal materials studied, it will eventually be possible to more accurately reconstruct past environmental conditions and determinme the role animals, especially the mollusks, played in the subsistence of the Indian.

At least 43 species of freshwater mussels were represented in the shell samples recovered at the CRBRP site. Of these 43, valves of six species (*Actinonaias ligamentina, Pleurobema cordatum, Fusconaia subrotunda, Cyclonaias tuberculata, Cyprogenia stegaria, Dromus dromas*) comprised 65% of all the identified mussel shell. Because of their generally large size, the first four would have provided probably the major portion of the meat derived from mussels. However, there was apparently no effort on the part of the individuals who gathered mussels to select only large adult specimens. Juveniles of several species such as *A. ligamentina* and *C. tuberculata* which are among the largest forms, as adults, occurring in the Tennessee River system, were represented in the samples. In addition, considerable numbers of typically small species, for example those of the *Epioblasma* complex, as well as quantities of gastropods, had also been collected by the site's inhabitants. The larger specimens of naiads are more easily observed, or felt when grubbing by hand, and the CRBRP site sample may conceivably reflect this. In all probability the CRBRP site sample reflects the former relative abundance of species inhabiting the shoals and gravel bars adjacent to the site.

Impoundment of the lower Clinch River, as well as all of the Tennessee River and its major tributaries, has detrimentally affected most of the huge mussel beds once found in these waters and has diminished the numbers of the few surviving species. Of the 43 species or forms represented in the CRBRP site samples, at least five are extinct and four are listed as Endangered Species (Bogan and Parmalee, 1983).

It is of interest to note that no speciments of the Three-horned Warty Back, *Obliquaria reflexa* (Rafinesque, 1820); Butterfly, *Ellipsaria lineolata* (Rafinesque, 1820); and the Pink, *Obovaria retusa* (Lamarck, 1819) were recovered in the CRBRP site samples. Today, the first two species occur locally throughout the Tennessee River system and the third very locally below Pickwick Landing Dam; all three were recorded from the lower Clinch before impoundment. The fact that the Fluted Shell, *Lasmigona costata* (Rafinesque, 1820); Fragile Papershell, *Leptodea fragilis* (Rafinesque, 1820); Pink Heelsplitter, *Potamilus alatus* (Say, 1817); and the Spectacle Case, *Cumberlandia monodonta* (Say, 1829), are missing in the samples also seems unusual since they do occur on or adjacent to shoals and gravel/sand bars in the larger rivers and are still found in the Clinch River above impoundment. If these naiads had inhabited the shoals adjacent to the CRBRP site when it was occupied, they must have been extremely rare.

The inequality of the quantity of shell recovered in the Early Woodland, Middle Woodland, and Mississippian components makes a comparison of species utilization by various groups who periodically occupied this site rather superficial. For example, of the approximately 23,900 mussel valves identified, about 85% were from the Middle Woodland components. Shells of *Fusconaia subrotunda, Cyclonaias tuberculata*, the *Pleurobema* complex, *Actinonaias ligamentina, Cyprogenia stegaria*, and *Dromus dromas* occurred with about the same frequency in both the Middle Woodland

and Mississippian samples. Combined, valves of these six species varied from approximately 56% (Mississippian) to 67% (Early and Middle Woodland) of the total number of shells in each component. Keeping the discrepancy of sample size in mind, there appears to have been little if any changes in the species composition of the mussel beds during the periods of occupation of the CRBRP site.

The aboriginal utilization of aquatic gastropods reflects two different areas of exploitation, with some differences in emphasis during the three subsequent occupations of the CRBRP site. *Leptoxis* spp. and *Io fluvialis* were collected in the riffle areas with good current, while *Pleurocera canaliculatum, Campeloma* spp. and possibly *Lithasia verrucosa* were obtained from eddy areas or backwater areas with little or no current and a cobble, mud or decaying vegetation substratum. The Early Woodland people apparently emphasized collecting from the shallow standing water close to shore, based on the fact that *P. canaliculatum, Campeloma* spp., and the two specimens of *L. verrucosa* represent 77% of the gastropod sample. During Middle Woodland times, the emphasis was on collecting the shallow backwater areas, but there was an apparent shift. Specimens from backwater areas still formed 77% of the sample, but *I. fluvialis* comprised 21% of the sample; this suggests that there may now have been an emphasis on collecting *I. fluvialis*, possibly because of its large size. The Mississippian sample is very similar to the Early Woodland, with 98% of the specimens reflecting quiet water-shore area exploitation with a marked decrease in the utilization of riffle species. These fluctuations in the relative importance of *I. fluvialis* in the samples may also be a reflection of fluctuations of the local population numbers.

The method of preparation of these gastropods is currently unknown. No pattern of breakage or evidence for roasting in fire was observed. Morrison (1942) makes the following statement in reference to *Campeloma* spp., but his comments may be expanded to cover all of the above noted gastropods:

> "These snails were in use for food as soon as the shell deposits began to accumulate, but there is no positive indication as to just how they were cooked, unless possibly they were steamed in a pit beneath the fire. Very few of the shells among thousands of individuals seen were fire marked, so we know they were not roasted over the fire."

Because of this lack of evidence of roasting or cooking in an open fire, and because there was no shell breakage pattern, it is reasonable to assume that gastropods may have been boiled in pots and consumed in the form of a broth.

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ISAAC LEA'S VIRGINIA NEOGENE SPECIES

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ABSTRACT

Isaac Lea's 1833 essay, "New Tertiary Fossil Shells from Maryland and New Jersey," described six new species: four mollusks, a barnacle, and a foraminiferan. However two substantive errors have plagued this work. Lea's New Jersey fossils were Pleistocene, not Tertiary, and his "Maryland" specimens from the Finch collection were actually collected in Virginia from the younger Yorktown strata. The recognition of correct provenance requires a reinterpretation of these species. *Balanus finchii* Lea is the senior synonym of *B. concavus proteus* Conrad, 1834; it is not conspecific with Pilsbry's (1930) figured "topotypes." The type of *Mactra clathrodon* Lea is a junior synonym of *Spisula modicella* (Conrad, 1833). Lea's supplemental specimens of *M. clathrodon* from Deal, New Jersey were most likely juvenile *Mulinia lateralis* (Say, 1822). *Acteon wetherilli* Lea, the type of *Acteocina* Gray (1847) is a junior synonym of *Acteocina canaliculata* (Say, 1822). *Rotella nana* Lea is a valid species of *Teinostoma. Fusus pumilus* Lea is a composite species based on two turrids and a mitrellid. As herein restricted, *F. pumilus* is the type of a previously unrecognized species of *Oenopota*, and becomes the first record of the genus in the Neogene of the Southeastern United States. Finally, *Miliola marylandica* Lea is a junior synonym of *Quinqueloculina seminula* (Linnaeus, 1767).

These conclusions are compatible with the now recognized Virginia source for all Finch collection species described by Thomas Say (1824), Morton (1829), Green (1830) and Conrad (1833).

Paleontologists studying the Eocene molluscan faunas of Alabama have long recognized the importance of Isaac Lea's (1833) *Contributions to Geology*, a work whose fine plates and extensive descriptions set an unrivaled standard of excellence for its time. This privately printed book was a compilation of one major essay, "Tertiary Formation of Alabama," and three essentially overlooked minor essays, "New Tertiary Fossil Shells from Maryland and New Jersey," "New Genus of Fossil Shells from New Jersey," and "Tufaceous Lacustrine Formation of Syracuse, Onondoga County, New York."

Lea was the first Amercian geologist to apply the Lyellian Tertiary epochs to various North American deposits. In the introduction to "Tertiary Formation of Alabama" Lea discussed the likely age of deposits from New Jersey to Alabama. He assigned strata at Yorktown, Smithfield, and Suffolk, Virginia to the Older Pliocene, an age which Rogers (1836) later disputed as too young. Most studies from 1837 to the 1970's have endorsed Rogers' Miocene assignment, but Akers (1972), using planktic foraminifera, has confirmed Lea's original Pliocene assignment.

Molluscs and barnacles listed in Lea's second essay, "New Tertiary Fossil Shells from Maryland and New Jersey," although catalogued by Brönn (1848), H. C. Lea (1848), and Sherbourne (1922-1933), were largely ignored by American systematists. Meek (1864) and Whitfield (1894) failed to include any citation of the species described by Lea.

Regarding these species, Lea stated:

> "I am under obligation to Mr. Finch for this (*Balanus finchii*, Lea, 1833) and many other species from St. Mary's. He very kindly placed them in my cabinet, shortly after his return from the examination of that celebrated deposit, about nine years since" (1833:211-212).

Further, of the portion of the Finch collection described by Thomas Say (1824), Ward and Blackwelder (1975:3-4) observed:

> "Most of the fossils described by Say at this time had been loaned to him by John Finch, a Scottish visitor to the United States. These fossils were mistakenly attributed by Say to Miocene deposits on the St. Marys River, Md. It is apparent from Say's descriptions, illustrations, and material that he had no Maryland collections in his possession at the Philadelphia Academy at this time. Finch's description (1833) of his own travels in America indicates that he probably shipped all the Maryland material he collected directly to England from

> one of the ports in Virginia. The materials which Say examined at the Philadelphia Academy of Sciences were probably collected on Finch's visit to the James River near City Point and the York River at Yorktown (Finch, 1833, pp. 266-275). The molllusks are all indicative of the Yorktown Formation of southeastern Virginia and northern North Carolina."

Ward and Blackwelder's (1975) conclusion, that the Finch collection taxa available to and described by Say came from the younger Virginian Pliocene strata, necessitates reconsideration of the "St. Mary's Maryland John Finch" specimens later described by Lea (1833), Morton (1829), Green (1830), and Conrad (1833). The confusion is understandable because Finch did collect Miocene age specimens from the rich shell beds along the St. Marys River, but those were shipped directly to London. (The apostrophe in "St. Mary's" is now archaic in geographic and geologic usage.) All of Lea's Finch types are housed in the Academy of Natural Sciences Philadelphia collections.

Lea's species in question are:

1. *Balanus finchii. "Description.* Shell short, conicocylindrical, smooth, nearly erect; substance of the shell rather thick; aperture nearly square; valves rather pointed above. Length, 5-20ths, Breadth .3, of an inch." (Lea, 1833:211) ANSP unnumbered.

Status: Balanus finchii was noted by Brönn, 1848, and Darwin, 1854, and was cited as a synonym of *B. concavus* Bronn, 1831 by Martin, 1904. Among the described Yorktown barnacles (see Ross, 1964), *B. finchii* is conspecific with *B. proteus* Conrad, 1834, a conclusion separately determined by Victor Zullo (1980, personal communication) from an examination of the types. Hence, *B. finchii* has priority over the more familiar *B. proteus* as the proper name for the common, strongly-ribbed Yorktown barnacle. Ross (1964) considered the Yorktown form subspecifically distinct from *B. concavus* Bronn; however, Zullo (1984) now references Lea's species to the genus *Concavus* (Newman, 1982), which would make the species *Concavus finchii* (Lea, 1833).

2. *Mactra clathrodon. "Description.* Shell subtriangular, thin, inequilateral, obscurely and transversely striate; beaks somewhat pointed; lateral teeth crossed by equidistant minute striae; excavation of the palleal (sic) impression small and rounded; anterior and posterior cicatrices scarcely visible; cavity of the shell somewhat deep; cavity of the beaks rather deep. Diameter .2, Length 5-20ths, Breadth 7-20ths, of an inch."

"St. Mary's, Maryland, John Finch." ANSP 3309.

"Deal, New Jersey." (Lea, 1833:212).

Status: Conrad (1838) and Brönn (1848) synonymized this species with *Mactra modicella* (Conrad, 1833) which had a few months priority. But Dall (1892:892) rejected this synonym, stating that *M. clathrodon* appeared to be a true *Mactra.* Glenn (1904:286) concluded, "Lea's type specimens are the young of the same species whose adult form Conrad later described as *M. subcuneata.*" Vokes (1957), in turn, observed *"M. clathrodonta* Lea" to be present in all three Maryland Miocene formations, and that it is the most common mactrid in the fauna. Undoubtedly Dall, Glenn and Vokes were influenced in their conclusions by the supposed St. Marys, Maryland source. However, I have compared the cotypes with juvenile Yorktown *Spisula modicella* (Conrad, 1833) of the same size and am convinced, like Conrad and Bronn, that Conrad's and Lea's taxa are conspecific. *Mactra clathrodon* is a junior synonym of *Spisula modicella,* and the Maryland species should properly be called *Mactra subcuneata* Conrad, 1838.

Lea's reference to a second specimen from Deal, New Jersey, introduces a new problem. No St. Marys Formation sediments have been reported in New Jersey, but older Calvert strata can be found in outcrops in the southern part of the state, and in the subsurface of the central and northern parts (Gibson, 1970:1818). Deal is located on the coast, a little south of Newark in the northern part of the state. Most systematists (e.g. Cernohorsky, 1978:83) have assumed that: (1) the Deal specimens were of the same provenance as the Finch material; and, (2) that the latter provenance is the Miocene St. Marys Formation of southern Maryland. It is now apparent that both assumptions are invalid.

Lea reported two species from Deal, the mactrid and a new species of opisthobranch snail, *Acteon wetherilli. Mactra subcuneata* Conrad extends down into the Calvert Formation, and could arguably have been responsible for Lea's "Deal" specimen of *"Mactra clathrodon."* However, there are no reported *Acteocina* from the New Jersey or Maryland Tertiary (Martin, 1904; Whitfield, 1894). The only alternative for Lea's Deal material compatible with the regional geology is the late Pleistocene which Richards (1962:45-46) reports as common in that area. The New Jersey marine Pleistocene contains common juvenile *Mulinia lateralis* (Say, 1822) whose morphology closely parallels *"Mactra clathrodon,"* and also common *Acteocina canaliculata* (Say, 1822) which supplied the type specimen (ANSP 14431) of *Acteon wetherilli.*The synonymy of *A. canaliculata* and *A. wetherilli* has been confirmed by Paul Mikkelsen (1984, personal communication), and is of special systematic interest because the two nominate taxa are respectively the designated types of the genera *Utriculastra* Thiele, 1925 and *Acteocina* Gray, 1847.

3. *Rotella nana. "Description.* Shell orbicular, flattened above, smooth, margin rounded; substance of the shell rather thin; spire nearly concealed; outer lip sharp; callus impressed in the centre, bounded by a fine impressed line; mouth nearly round. Length 1-20th, Breadth nearly .1, of an inch." (Lea, 1833, 214) ANSP 1569.

Status: Gardner (1948: pl. 25, figs. 23-24) has illustrated the type. "*Teinostoma nana* (Lea, 1833)" has been used for very small, low-domed teinostomes with a heavy umbilical callus and a suture that partially overlaps the spire. Such shells are found in the St. Marys, Yorktown and Duplin Formations. These populations appear conspecific, although a detailed study of large populations may eventually prove them to be distinct.

4. *Fusus pumilus. "Description.* Shell ovately fusiform, longitudinally ribbed; substance of the shell thin; spire rather obtuse; suture imperssed; whorls four, slightly convex; columella slightly twisted; canal short; mouth narrow. Length .1, Breadth 1-20th, of an inch." (Lea, 1833) ANSP 13827.

Status: The listings of H. C. Lea (1848), Brönn (1848) and Sherbourne (1922-1933) appear to be the only subsequent references to this species. The type lot consists of three specimens glued to a card. Each is a distinctly different species, and both the original description and figure are composites. Lea (Fig. 226) shows the spire form of the left specimen, the canal of the middle, and the sculpture of the right-hand specimen. The specimen on the left was at first judged to be specifically indeterminate mangelid; the specimen to the right is another indeterminate juvenile turrid. The center specimen is a broken but recognizable juvenile of the common, often cited, and widespread *Mitrella communis* (Conrad, 1862). Restricting the type of *F. pumilus* to this second (middle) specimen would have the advantage of establishing a certain identity, but *Mitrella communis* is well entrenched in the literature, and stability would not be served by such action.

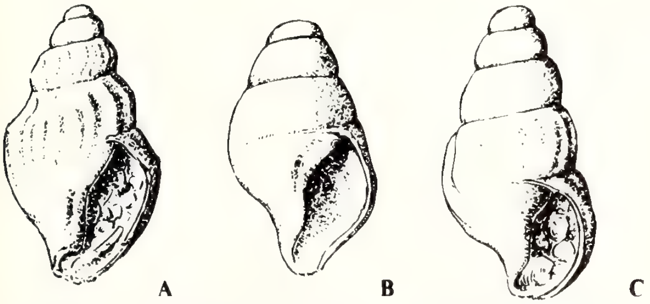

Fig. 1A. Left syntype of *Fusus pumilus* I. Lea, 1833, herein designated lectotype of *Oenopota pumilus* (I. Lea, 1833). Length 1.9 mm. **B.** Center syntype of *Fusus pumilus* I. Lea, 1833, a juvenile specimen of *Mitrella communis* (Conrad, 1862). **C.** Right syntype of *Fusus pumilus* I. Lea, 1833, a juvenile turrid of uncertain species. Figure drawn by Carol Jones.

At my request (1982), Virginia Orr Maes examined the lot and determined that the specimen shown here as Figure 1A belonged to *Oenopota*, a boreal genus of small mangelid turrids. This specimen is designated herein as the lectotype of *Fusus pumilus.* So restricted, *Oenopota pumilus* (I. Lea, 1833) L. Campbell, 1985 is a minute turrid with a small smooth protoconch, and a total of five whorls. The shell is relatively broad, with a slight angulation of the periphery. Visible sculpture (the type is varnished) consists of about eighteen narrow, axial riblets per whorl which are most prominent just above and below the angulation of the whorl. Aperture is large, the outer lip broken. Size: 1.9 mm. Type locality: Virginia. Type: ANSP 13827a.

This is the first record of *Oenopota* in the Neogene of Eastern North America. It has escaped detection because it is very small, easily confused with juveniles of the many other Yorktown Formation turrid species, and finally, as a Boreal genus, it is out of habitat in the warm-temperate to subtropical Yorktown fauna, and therefore predictably rare.

5. *Miliola marylandica. "Description.* Shell elliptical, depressed in the middle, rounded at the edges, lobes in contact; mouth small, round, terminal, furnished with a large tooth. Length 1-20th, Breadth nearly 1-20th, of an inch." (LEA, 1833:215) ANSP unnumbered.

Status: Bagg, 1904, correctly synonymized this species with *Quniqueloculina seminula* (Linné,1767), a common Yorktown and recent species also found in the St. Marys Formation.

CONCLUSIONS

The Virginia source demonstrated by Ward and Blackwelder (1975) for Thomas Say's (1824) "John Finch, St. Mary's" species can now be applied to all species of the John Finch collection which were described by contemporary American systematists. These include *Conus marylandicus* Green, 1830, unknown in Maryland but locally common in the Virginia Yorktown Formation; *Spisula confraga* (Conrad, 1833) which is reported from Maryland but is more common in the Yorktown; *Crepidula costata* Morton, 1829 (not *C. costata* Sowerby, 1824) which is locally abundant in the Yorktown; and five of the six new species described by Isaac Lea (1833). Lea's Finch collection species are *Concavus finchii*, a valid species of barnacle known only from Virginia and North Carolina; *Mactra clathrodon*, a junior synonym of *Spisula modicella* (Conrad, 1833); *Teinostoma nana*, a valid microgastropod species; *Fusus pumilus*, a previously unrevised composite species herein placed in *Oenopota*, a turrid genus; and *Miliola marylandica*, a foraminiferan and junior synonym of *Quinqueloculina seminula* (Linné,1767). *Oenopota pumilus* is presently known only from the unique lectotype, but the remaining four Lea taxa are common and are unique to, or more common in, the Yorktown Formation. *Acteon wetherilli* Lea, 1833, was not a part of the Finch collection, but rather came from the Pleistocene of Deal, New Jersey. Lea misidentified a Deal juvenile *Mulinia lateralis* (Say, 1822) as conspecific with his *Mactra clathrodon*, therefore presuming the New Jersey and St. Marys Miocene (actually Virginia Pliocene) faunas to be contemporaneous. *A. wetherilli* is a Pleistocene junior synonym of *Acteocina canaliculata* (Say, 1822).

In "New Tertiary Fossil Shells from Maryland and New Jersey" Isaac Lea thus committed two errors: his New Jersey fossils were not Tertiary, and his Tertiary fossils were not from Maryland. After one hundred and fifty years of confusion, recognition of true provenance allows accurate interpretation of these species for the first time.

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INTERNATIONAL SYMPOSIUM ON THE ECOLOGY OF LARVAL MOLLUSCS

ORGANIZED BY

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AMERICAN MALACOLOGICAL UNION
NORFOLK, VIRGINIA
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THE INTERNATIONAL SYMPOSIUM ON THE ECOLOGY OF LARVAL MOLLUSCS: INTRODUCTION AND SUMMARY

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Working on molluscs, I am continually impressed with the potential for research on comparative larval ecology. Molluscan species fill a broad ecological spectrum from infaunal species and sedentary oysters to pelagic squids and pteropods. Included are marine, freshwater, and terrestrial forms. Not only do molluscs represent varied evolutionary backgrounds (Shuto, 1974; Scheltema, 1978; Scheltema and Williams, 1983), but their fossil record allows inferences on ancient larval ecology (e.g. Kauffman, 1975; Lutz and Jablonski, 1978; Jablonski and Lutz, 1980; Hansen, 1978; 1980; Bouchet, 1981; Powell *et al.,* 1984).

This symposium grew out of the frustration I experienced in attempting field studies of comparative larval ecology (Vecchione, 1979; Vecchione and Grant, 1983). The causes of this frustration were serious taxonomic problems and a literature base that was scattered and often difficult to obtain. Larval development has been adequately described for only a small percentage of molluscan species known to have planktonic larvae. Many of the existing descriptions are of little use for definitive identification of specimens in plankton samples. Although some very useful studies describe veligers of molluscs (e.g. Loosanoff *et al.,* 1966; Chanley and Andrews, 1971), many are unpublished theses (e.g. Taylor, 1975) or individual articles either in broad-spectrum journals (e.g. Lebour, 1937; 1945; Sullivan, 1948; Rees, 1950; Richter and Thorson, 1975; Pilkington, 1976; LePennec, 1980; Lutz *et al.,* 1982; Thiriot-Quievreux and Scheltema, 1982; Thiriot-Quievreux, 1983) or in symposia proceedings and other publications with limited distribution (e.g. Jorgensen, 1946; Thorson, 1946; Fretter and Pilkington, 1970).

Presently, the base of literature on larval studies from many diverse phyla is expanding rapidly. General questions are being defined for which tests of hypotheses will allow development of early-life-history theory (e.g. Vance, 1973; Obrebski, 1979; Jackson and Strathmann, 1981; Keough and Downes, 1982; Roughgarden *et al.,* 1985). For instance, within available resources how can a species adapt so that energy can be allocated adequately to reproduction and other functions? Is the function of a larval stage to allow dispersal and colonization, to take advantage of resources that would not be available with direct development (e.g. near-surface phytoplankton), or to minimize intra-specific competition between adults and offspring? Whatever the role of the larval stage, both benthic and pelagic species with planktonic young face the requirement of either retention within the adult habitat or recruitment to suitable areas. Determining the evolutionary solution to the retention vs. recruitment dichotomy involves elucidation of behavioral mechanisms (e.g. Mileikovsky, 1973; Richter, 1973), defining cues and responses (e.g. Cole and Knight-Jones, 1939; Scheltema, 1961; Thorson, 1966; Crisp, 1967; Hidu, 1969; Hidu and Haskins, 1971; Cragg and Gruffydd, 1975; Mann and Wolf, 1983). The choice between retention and recruitment will affect population phenomena such as gene flow (Scheltema, 1971; 1975) which, in turn, affects speciation and higher-level systematics over geological time (Jablonski, 1982; Hansen, 1983).

For species with a free-living larval stage, larval mortality may be a particularly important factor in population dynamics (Thorson, 1950). Potential sources of larval mortality currently receiving much attention include starvation (e.g. Beyer, 1980; O'Connell, 1980; Anger *et al.,* 1981), predation (e.g. Mileikovsky, 1974; Burrell and Van Engel, 1976; Steinberg and Kennedy, 1979), pollution (e.g. Roosenburg *et al.,* 1980; Wright *et al.,* 1983), and "wastage" due to transport into unfavorable areas (e.g. Smyth, 1980; Norcross and Shaw, 1984). Any of these phenomena will affect recruitment, both in the fisheries sense and in the biological sense. Thus, population size of a species may (or may not: Watzin, 1983) be strongly linked to larval ecology (Thorson, 1966).

Much of the conceptual development behind these questions is based on classical studies of larval molluscs. The problems of retention of oyster larvae within the commercial fishing grounds have received much attention (Carriker, 1951; Pritchard, 1952; Wood and Hargis, 1971; Seliger *et al.,* 1982). Scheltema's (1971) pioneering work on delay of metamorphosis, contrasting the biogeographic potential of species having teleplanic larvae with those having actaeplanic larvae, has formed the framework of studies based on many phyla (e.g. Scheltema, 1975; Laursen, 1981; Rice, 1981; Domanski, 1984). Thorson (1950) relied heavily on prosobranch gastropods to detail the overall relationship between developmental modes and latitude. Postlarval events that are a continuation of the larval history were pointed out for young mussels (Bayne, 1964) and still constitute a subject ripe for research (e.g. Sigurdsson *et al.,* 1976; Luckenbach, 1984; Petersen, 1984; Prezant and Chalermwat, 1984). Conversely, the possible effects of starvation and "larval wastage", which have been shown to be quite important in the life histories of species in other phyla, have been largely neglected in studies of larval molluscs (Vecchione, 1981; in press).

Although I must confess a substantial ignorance of freshwater molluscs, it seems to me that the developmental patterns unique to this group should allow interesting comparative studies, not only on larval ecology but also on the evolution of parasitism.

This symposium was organized to assemble as diverse a group of researchers as possible. Topics included distribution, physiology, behavior, and taxonomy. As many taxa and habitats were included as possible, as were both basic and applied studies. My primary goal in organizing the symposium was to get people from many backgrounds talking together.

This goal was fulfilled by a truly international assemblage of scientists. In all, 17 papers were presented, representing the work of 29 authors from seven countries. Of these papers, six are presented in their entirety in this issue. Several authors had plans to publish their work elsewhere whereas others are continuing data collection and analyses. Some of these studies are presented here as expanded abstracts.

Probably the most delightful parts of this symposium for those of us who attended were the many discussions after papers, in hallways and eating places, and during the "round-table" session that concluded the symposium. One purpose of the "round-table" was to compile a list of recommendations that participants felt were important topics for future research. The following are the recommendations proposed and agreed upon by those in attendance.

(1) *Careful systematic studies of larvae.* There was a strong consensus among the participants that thorough studies of larval taxonomy and systematics are needed and are basic to the study of larval ecology.

(2) *Postlarval transport processes.* Many participants had observed that planktonic transport of postlarval molluscs is a widespread though largely undocumented phenomenon. Potential mechanisms mentioned for such transport include "byssus-drifting", production of mucous threads for resuspension by currents, rafting on floating material, and dispersal on surface tension.

(3) *Interaction of recruitment and larval/postlarval phenomena.* Recruitment may be affected either by larval (planktonic) phenomena or by postlarval (benthic, or as in (2) above, planktonic) phenomena. Many participants felt that since the early benthic phase is actually meiofaunal in size, this phase has been inadequately investigated and specific studies should be designed using meiofaunal techniques (e.g. Muss, 1973).

(4) *Comparative studies of larval ecology.* Hypotheses about larval ecology can effectively be tested by comparative studies using sibling species with different developmental adaptations or by similar comparisons among higher taxa (e.g. Ament, 1979).

(5) *Combined laboratory and field studies.* Cross-verification is needed between observations resulting from field and laboratory studies. Empirical work in the field can develop specific questions that may be testable under controlled laboratory conditions, and laboratory experiments may serve as a useful guide for the design of field sampling programs. Such combined studies would more effectively estimate the range of potentials of which larvae are capable.

(6) *Alternate hypotheses for developmental types.* The function of the larval phase in a species' life history is often assumed (e.g. feeding vs. dispersal vs. the necessity to attain an adequate size to metamorphose or set). Tests must be designed to examine the appropriateness of such assumptions.

(7) *Genetics of poecilogony and yolk dynamics.* Is a species capable of altering its developmental pattern among planktotrophy, lecithotrophy, and direct development (Robertson, 1974) and, if so, are such alterations reversible? Current evidence on poecilogony, or developmental plasticity, ranges from equivocal to contradictory.

(8) *Assumptions of applied ecology.* Frequently, applied disciplines, such as fisheries science or pollution ecology, base predictions on assumptions about larval ecology of questionable validity. Although the participants recognized that this is often a requirement when decisions must be made and the necessary data do not exist, these assumptions should be carefully examined and, when necessary, tested.

A symposium introduction is not the proper forum for a thorough review of larval ecology. My purpose here has been simply to show that we who work with larval molluscs are building on a broad foundation. This foundation is the work of the many researchers mentioned above and many others omitted because of the constraints of an introductory overview. I hope that publication of this symposium will provide stimulus and direction for equally varied and interesting work.

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LARVAL ECOLOGY OF MOLLUSKS AT DEEP-SEA HYDROTHERMAL VENTS

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ABSTRACT

Modes of larval development of thirty species of mollusks (gastropods and bivalves) from three deep-sea hydrothermal vent sites in the Eastern Pacific (21°N, 13°N and the Galapagos Rift) have been inferred from analyses of larval shell morphologies. Only three species (one mytilid and two turrids) have morphologies indicative of planktotrophic, high dispersal modes of development; the remaining twenty-seven species apparently have managed to persist in the ephemeral and patchy vent environments despite the possession of nonplanktotrophic, seemingly low-dispersal modes of development. From analogies with related, shallow-water species having comparable larval shell morphologies, the free-swimming stage of those species having nonplanktotrophic development remain in the plankton for only a few hours to a few days. If this is indeed the case for hydrothermal vent species, larval dispersal between vents may proceed via a stepwise process. Alternatively, the cold, ambient bottom waters of environments away from the immediate vicinity of the vents may lower metabolic rates, permitting nonplanktotrophic larvae to remain in the plankton for far longer periods of time than their shallow-water analogues. Such a reduction in developmental rates would increase dramatically the dispersal capability of these organisms.

Chemoautotrophically-based biological communities associated with deep-sea hydrothermal vents have been the subject of considerable research since the discovery of these faunal assemblages in 1977 (Lonsdale, 1977; Grassle *et al.*, 1979; Jones, 1985). One of the fundamental questions concerning the ecology and biogeography of the vent biota is how the relatively sedentary organisms at the vents locate and colonize these ephemeral and patchy environments. Larval ecological studies conducted to date on the hydrothermal vent organisms have been, by necessity, entirely inferential and focused on three groups of organisms: mollusks (Lutz *et al.*, 1980, 1984; Turner and Lutz, 1984), decapod crustaceans (Van Dover et al., 1984, 1985), and ampharetid polychates (Desbruyères and Laubier, 1982, 1984; Zottoli, 1983). Initial studies, based on analyses of the larval shell morphology of a large mytilid (Kenk, 1979; Le Pennec et al., 1983) present at several East Pacific hydrothermal vent sites, indicated that one of the dominant (in terms of biomass) members of the macrofauna undergoes a planktotrophic, high-dispersal mode of larval development (Lutz *et al.*, 1980). Subsequent studies, however, have indicated that many of the other vent organisms, both macro- and microfaunal, do not require a high-dispersal stage to persist in these transient and geographically-isolated environments and have suggested that the reproductive strategies in the hydrothermal vent community are more complex than previously believed

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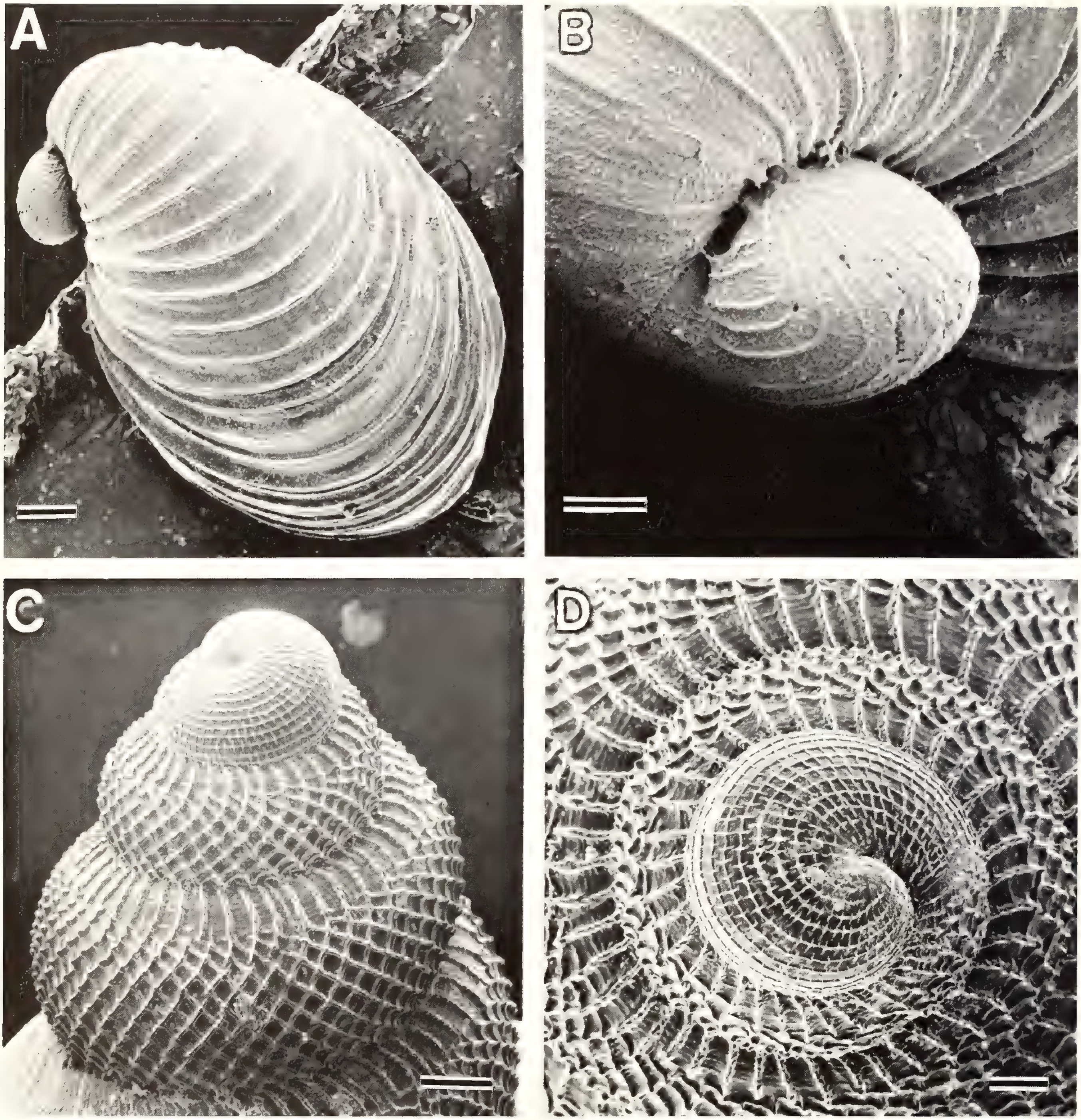

Fig. 1. Scanning electron micrographs of the shells of juvenile gastropods from deep-sea hydrothermal vents. (A) Archaeogastropod limpet present at both the 13ºN and 21ºN hydrothermal vent sites. Scale bar, 100 μm. (B) Protoconch morphology of (A). Scale bar, 50 μm. (C) Larval shell (protoconch I and II) morphology of neogastropod turrid from the 21ºN hydrothermal vent area (only one specimen of this species was collected from the site). Scale bar, 100 μm. (D) Apical view of (C). Scale bar, 50 μm.

(Lutz *et al.*, 1984). In the present paper, we will present further evidence that suggests that the vast majority of organisms present at the vents undergo nonplanktotrophic development, with a relatively restricted, low-dispersal larval stage. Our studies are based entirely on analyses of the shells of molluscs, which are the only taxa present at the vents that preserve within their skeletal tissues a record of early ontogenetic history (see Jablonski and Lutz, 1980, 1983 for details concerning the utility of the molluscan shell for inferring modes of larval development).

MATERIALS AND METHODS

Samples were collected from the Galapagos Rift and 21°N sites (Corliss and Ballard, 1977; Ballard and Grassle, 1979; Corliss et al., 1979; Grassle *et al.,* 1979) using the deep-sea research vessel *Alvin* and from the 13°N hydrothermal fields (Desbruyères et al., 1982) using the submersible *Cyana.* Minute mollusks, with at least portions of their prodissoconchs or protoconchs intact, were isolated from the washings of biological and geological samples. The specimens were immediately fixed in a 5-10% buffered seawater formalin for various lengths of time and subsequently preserved in 70-95% ethanol. Shell preservation was best for those specimens fixed in the formalin for less than 48 hours and subsequently preserved in 95% ethanol. Cleaned specimens either were: (1) immersed in a 5% solution of sodium chlorite for one to ten minutes, rinsed in distilled water, and subsequently air-dried; or (2) dehydrated in a graded series of acetone or ethanol and subsequently critical-point dried. Dried specimens were mounted on copper tape, coated (under vacuum) with approximately 400 Å of gold-palladium or a combination of gold and carbon and examined under one of several scanning electron microscopes (e.g., AMR 1000, ETEC Autoscan).

Modes of larval development were inferred on the basis of protoconch or prodissoconch size and form utilizing criteria summarized by others (for reviews, see Ockelmann, 1965; Shuto, 1974; Scheltema, 1978; Bouchet and Warén, 1979; Jablonski and Lutz, 1980, 1983).

RESULTS AND DISCUSSION

While a complete list of the molluscan species sampled to date from the three hydrothermal sites awaits the completion of further detailed taxonomic studies, a conservative estimate places the number of retrieved species at 41. Of these, 24 have been collected from the 21°N site, 23 from the 13°N site, and 13 from the Galapagos site. Seven of the species are present at each of the sites and, of the 13 species present in the Galapagos vent fields, all but three (two small, unidentified bivalves and one turrid, each represented by a single specimen, suggesting that these organisms may not be "characteristic" vent fauna) were present at the 13°N site. Fifteen of the species collected were present at both the 13°N and 21°N sites.

Thirty of the 41 species present at the three sites had larval shells sufficiently well-preserved to infer modes of development (e.g., Figs. 1-3). Only three of these (two turrids, both of which may well be present in "nonhydrothermal" deep-sea environments, and the vent mytilid) have protoconch or prodissoconch morphologies reflective of planktotrophic development (Fig. 1C,D). Each of the remaining 27 species (24 gastropods and 3 bivalves) have larval shell morphologies indicating a nonplanktotrophic mode of development. All of the gastropods have a protoconch I with fewer than one-and-a-half whorls and lack a protoconch II; maximum protoconch I dimensions range from 175 to 325 μm (Figs. 1A,B, 2). Comparison with the larval shell morphology of archeogastropod limpets, neogastropod turrids and trochacean archaeogastropods for which development is known suggests that most or all of the vent gastropods undergo nonplanktotrophic development with a free-swimming, but nonfeeding larval stage (Rodriguez Babio and Thiriot-Quiévreux, 1975; Fretter and Graham, 1977; Strathmann, 1978; Lindberg, 1979; Heslinga, 1981; Bandel, 1982, Jablonski and Lutz, 1983). A possible exception is a species with a protoconch of 325 μm, which indicates development from a large, yolky egg and perhaps direct development with the absence of any free-swimming stage. Each of the specimens of the three species of unidentified, juvenile bivalves retrieved from the sites and depicted in Fig. 3 have a large prodissoconch I (lengths ranging from 210 to 350 μm) and little or no prodissoconch II. Such morphologies are characteristic of species having nonplanktotrophic modes of development (for discussion, see Ockelmann, 1965; Jablonski and Lutz, 1980, 1983). One species for which no well-preserved, positively-identified juvenile specimens were available was the giant vent clam, *Calyptogena magnifica* (Boss and Turner, 1980), which was present at all three of the vent sites (only empty valves at 13°N). While the lack of an intact prodissoconch prevented interpretation of larval shell morphological features, the maximum diameter of 309 μm recently reported for the large, yolky egg of this species (Boss and Turner, 1980) strongly suggests the existence of a nonplanktotrophic larval stage.

On the basis of the above results we conclude that nonplanktotrophic development with a free-swimming, but nonfeeding, larval stage is the rule, rather than the exception, at deep-sea hydrothermal vents. Given a nonplanktotrophic larval dispersal stage, it is remarkable that 10 of the 13 species present at the Galapagos site are also present at either 13°N or 21°N, despite the large distances between the various sites (the 21°N and Galapagos sites are separated by 3300 km and yet share seven molluscan species). If, as in the case of closely-related, shallow-water species, the larvae remain in the plankton for only a few hours to a few days (see Webber, 1977; Heslinga, 1981; Jablonski and Lutz, 1980, 1983), it would appear most likely that the larvae of the majority of the vent organisms must disperse in a stepwise manner. At the present time, however, our knowledge of deep-ocean circulation patterns and the distribution of active vent areas along midocean ridge systems is insufficient to determine whether or not such dispersal might be feasible. Alternatively, cold, ambient bottom temperatures may sufficiently lower metabolic rates of the larvae to permit dispersal over far greater distances. Clearly more biogeographical data, further benthic, as well as planktonic, surveys, and additional laboratory studies concerning the relationship between temperature and duration of nonplanktotrophic dispersal stages are necessary before we can fully understand the role of larval ecology in the origination and persistence of hydrothermal vent species.

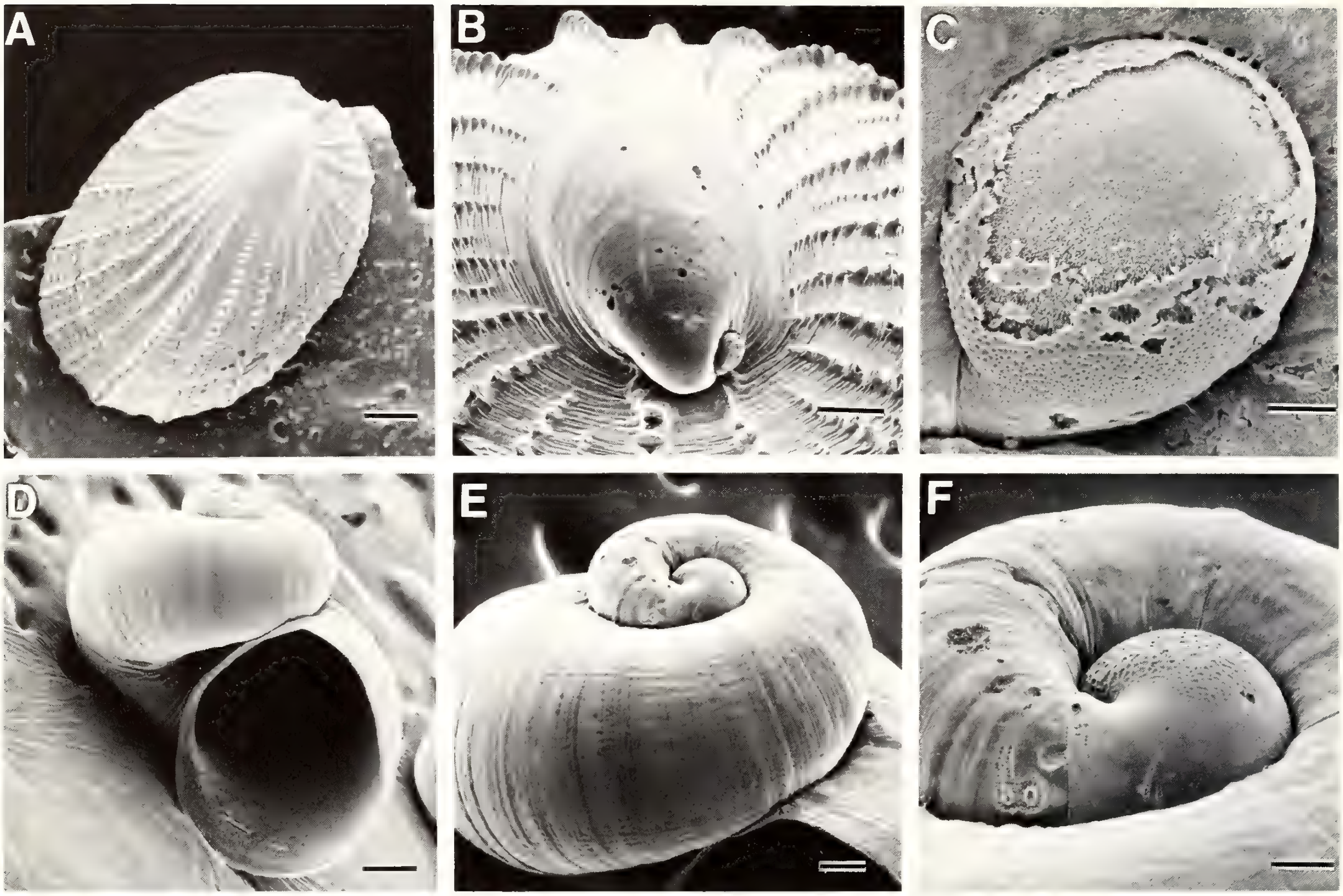

Fig. 2. Scanning electron micrographs of the shells of juvenile gastropods from deep-sea hydrothermal vents. (A) Archaeogastropod limpet present at all three of the studied hydrothermal vent sites (Galapagos Rift, 13ºN and 21ºN). Scale bar, 400 μm. (B) Apical view of (A). Scale bar, 200 μm. (C) Protoconch of (A). Scale bar, 25 μm. (D) Coiled trochoid archaeogastropod present at both the 13ºN and 21ºN sites. Scale bar, 200 μm. (E and F) Higher magnifications depicting protoconch of (D). Scale bars, 100 μm and 50 μm, respectively.

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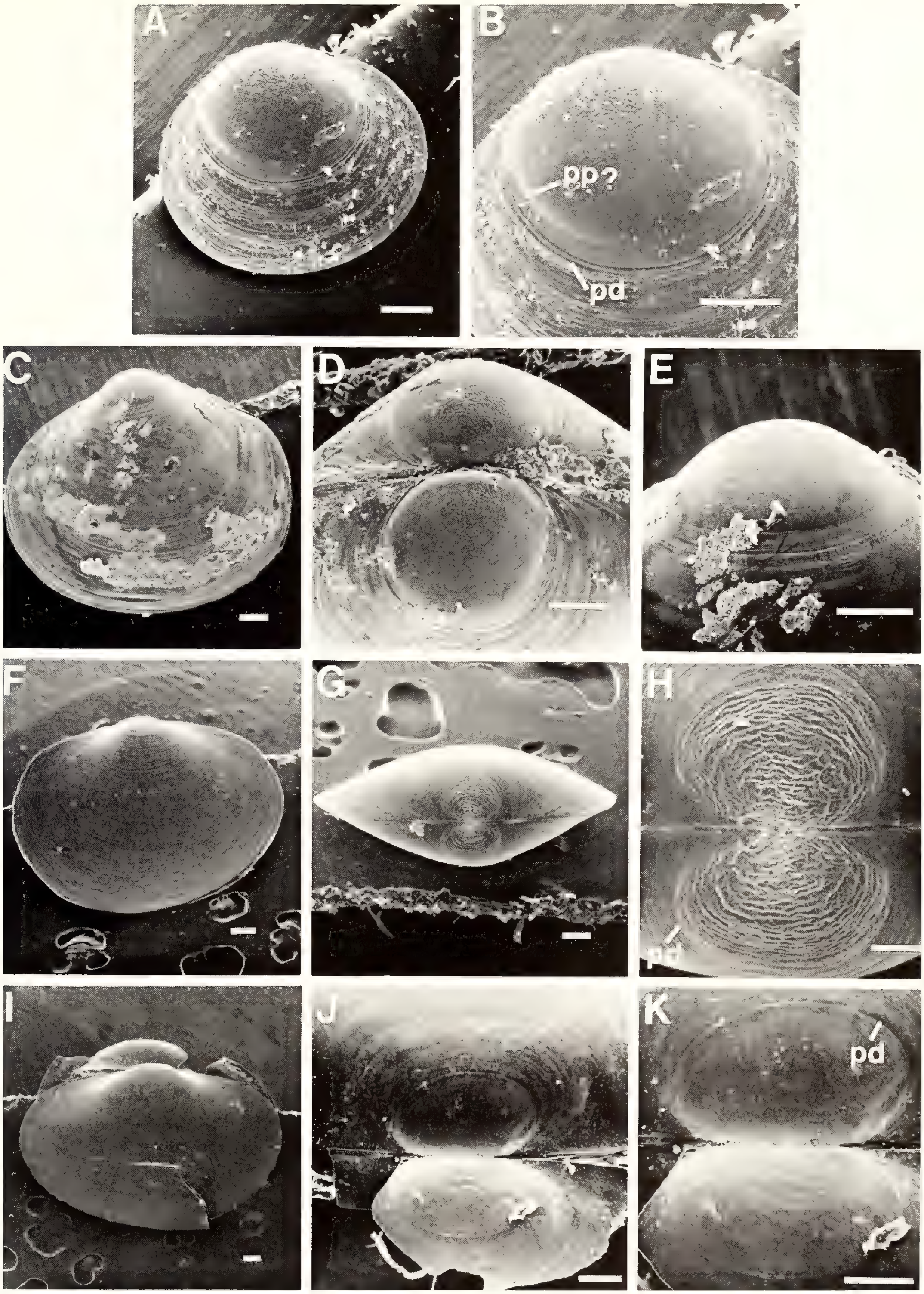

Fig. 3. Scanning electron micrographs of the shells of juvenile bivalves from deep-sea hydrothermal vents. (A,B) Early postlarval specimen collected from the 21ºN hydrothermal vent area. Scale bars, 100 μm. (C-E) Juvenile specimen collected from the 21ºN hydrothermal vent area. Same species as that depicted in Figs. A and B. Scale bars, 100 μm. (F-H) Juvenile specimen collected from the Galapagos Rift hydrothermal vent area (Mussel Bed site). Scale bar for F and G, 100 μm; scale bar for H, 50 μm. (I-K) Juvenile specimen collected from the Galapagos Rift hydrothermal vent area (Mussel Bed site). Scale bars, 100 μm. Abbreviations: pd, prodissoconch-dissoconch boundary; pp, prodissoconch I/II boundary.

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THE LOCOMOTION AND ENERGETICS OF HATCHLING SQUID, *ILLEX ILLECEBROSUS*

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ABSTRACT

Although never seen in nature, gelatinous egg masses up to 1 m in diameter containing 10,000 to 100,000 eggs have been produced in captivity by female *Illex illecebrosus* swimming in mid-water in the 15 m diameter Aquatron pool. When incubated at temperatures between 13 and 26°C these masses produced viable hatchlings whose behaviours were observed and recorded. The hatchlings sink at 5 mm s^{-1}, swim vertically at speeds up to 26 mm s^{-1}, hover and avoid both the surface and the bottom. Metabolic rates estimated from rates of yolk utilization and calculated values for swimming costs were used to predict "critical periods" or survival times for unfed hatchlings in various temperature and activity regimes. These are discussed in relation to the hypothesized role of the Gulf Stream in distribution of the hatchlings of this commercially important but still poorly understood squid species. Potential benefits from vertical migration are suggested and a comparison with *Loligo opalescens* made.

The ommastrephid squid, *Illex Illecebrosus* (Lesueur), occurs in the western North Atlantic Ocean from the Labrador Sea south at least to central Florida, and has produced catches exceeding 100,000 metric tons in its northern range during several recent years. Its life cycle is not well known, but there is evidence that the major stocks which feed during the summer on the Scotian Shelf and Grand Banks come from juveniles found in late winter in the upwelling zone along the northern edge of the Gulf Stream (O'Dor, 1983) and that adults from these stocks migrate south in the fall (Dawe *et al.,* 1981). This is probably a spawning migration to warm waters since eggs fail to develop at temperatures below 12°C (O'Dor *et al.,* 1982), and, as this report indicates, develop well at temperatures up to 26°C. The spawning sites are unknown, and while earlier literature suggests demersal spawning (Hamabe, 1962; 1963), recent observations suggest that mid-water spawning of large neutrally buoyant egg masses in the Gulf Stream is a plausible alternative (O'Dor and Balch, 1985).

The behaviours and metabolic patterns required to survive in the open ocean at 20 - 25°C should be quite different from those required to survive near the bottom on the continental shelf at 13°C. This study examines the behaviour of newly hatched *I. illecebrosus* in the laboratory and uses data on yolk absorption rates, standard metabolic rates and swimming speeds to estimate the "critical periods" of hatchlings under a variety of temperature and activity regimes. The consequences for animals in nature are then briefly considered. Similar data for *Loligo opalescens* Berry are examined and compared to test the applicability of the approach.

MATERIALS AND METHODS

ANIMALS

Adult squid were held in the 15 m diameter, 3 m deep pool at the Aquatron Laboratory under conditions that induce precocious maturation and spawning (O'Dor *et al.,* 1977). Reports on the characteristics of the tenuous gelatinous egg masses, which are typically spherical and between 0.5 and 1.0 m in diameter, have appeared elsewhere (Durward *et al.,* 1980; O'Dor and Balch, 1985). Intact egg masses can be collected from the pool and incubated at controlled temperatures. A long-handled triangular sheet-metal funnel, 1 m on a side at the outside edge, was used to "scoop" a mass off the bottom and direct it into a bag, 0.5 m in diameter and 1 m long, made of black nylon window screen. The bag was attached to the funnel with Velcro; once a mass had been raised near the surface it was detached and the open end sealed with the Velcro. A polyethylene drum liner (200 *l*) was lowered beneath the enclosed mass, and an entire mass, still suspended in water, could be lifted out using a crane. For studies of egg development rate, an enclosed mass was left suspended in the liner and a gentle flow of constant temperature water introduced (16, 21, and 26°C).

Newly hatched squid have a mantle length of about 1.2 mm and easily escaped through the screen around the mass. The overflow from the liner was allowed to flow upward through a 1 *l* settling cone covered with 0.5 mm mesh nylon netting to retain the hatchlings. The velocity gradient produced as the water ascended the cone allowed the squid to find a level where they could swim comfortably. At intervals squid were removed and placed in other holding tanks or experimental systems.

TECHNIQUES

Behavioural observations were recorded in either a standard 20 *l* glass aquarium through a 50 mm lens or in a vertical flow-through swim chamber (3 mm square and 78 mm high, made from microscope slides) through a Zeiss dissecting microscope at 5x with the ocular replaced by an RCA TC 2011/N low-light video camera which was connected to a Sony SLO-323 Beta recorder. A Vicon Industries Model V240 Date/Time Display Generator was used to add a time base to the nearest 0.1 s to the recording. Frame-by-frame analysis was used to calculate swimming velocities. Squid at various stages, both pre- and posthatch, were photographed in plastic petri dishes through a Zeiss inverted microscope from top and side views, and the volume of yolk remaining calculated by summing the volumes of various segments (usually cylinders or cones) representing the yolk mass using standard mensuration formulae.

CALCULATIONS

Direct measurements of the cost of locomotion in hatchlings has not yet been possible, but Daniel (1983) has given a detailed analysis of medusan jet propulsion that resembles that of *I. illecebrosus* hatchlings. The Reynolds numbers (R_e) for the squid are in the same range (1 to 500), and the drag coefficient (C_d) can therefore be estimated from the equation:

$$C_d = 24/R_e^{0.7}$$

From this the drag force (D), the major force the squid have to overcome, can be estimated from the equation:

$$D = 0.5\ C_d\ p\ S\ u^2.$$

Where p is the density of water, S is the frontal surface area and u the velocity of the squid. The power consumption (P) to overcome drag is then:

$$P = D\ u$$

Solutions of these equations in S.I. units gives power in watts that have been converted in calories per day for comparison with other biological data (1 watt = 20,635 cal d^{-1}). The metabolic energy consumed is not, of course, equal to mechanical output, so these values must be adjusted for efficiency. Daniel found typical efficiencies in medusae in the range of 5 to 10%, while O'Dor (1982) found efficiences for adult squid of about 4%; here 5% efficiencies have been assumed for hatchlings.

The only direct measurements of metabolic rates in hatchling squid are those of Hurley (1976) which are for "routinely" active *Loligo opalescens*. These values are similar to routine weight-specific metabolic rates for adult *L. opalescens*, and it appears reasonable to assume the same metabolic rates in other hatchlings as in adults of the same species since in many cases the weight exponents for squid have not proved to be significantly different from 1.0 (O'Dor and Wells, 1985). On this basis, standard metabolic rates at 15°C of 303 and 257 ml O_2 $kg^{-1}h^{-1}$ for *I. illecebrosus* (Webber and O'Dor, 1985) and *L. opalescens,* respectively, have been used for hatchlings. Assuming 1 ml O_2 equals 4.6 cal and no diel changes, this equals 33.4 cal $g^{-1}d^{-1}$ for *I. illecebrosus* and 28.4 for *L. opalescens.*

RESULTS

OBSERVATIONS OF PRE- AND POSTHATCH *I. ILLECEBROSUS*

Once the embryos reached stage XVII of development (O'Dor *et al.,* 1982), some activity was seen inside the egg. Mantle contractions occurred in bursts of 7 to 14 followed by a period of rest. There appeared to be no preferred orientation in the egg; the embryos rotated in a figure-eight, powered by a combination of ciliary motion, weak mantle contractions and an occasional jet. As the embryos developed further, the mantle contractions become stronger but less spasmodic. Animals that hatched before stage XX of development still had weak mantle contractions and were not sufficiently coordinated to produce jetting sequences. Consequently, these animals could not leave the bottom of the container. Stage XX hatchlings jetted up through the water column to the surface at speeds up to 26 mm s^{-1} (the maximum speed measured during a single jet was 52 mm s^{-1}), but averaged about 10 mm s^{-1}. They could hover in one place by bobbing up and down, but had very limited ability to control lateral movements. The fins always point toward the surface, whether the animal is jetting or sinking. This orientation may be due to the position of the two statoliths in the head behind the optic lobes which would have a higher density than tissue. When a hatchling was not jetting it would sink at about 5 mm s^{-1} and, upon touching the bottom, immediately jet upward. The first contact with the bottom was with the proboscis (fused tentacles peculiar to young of the family Ommastrephidae, which appeared to extend and push the animal off like a pogo-stick. When a hatchling touched the water surface it relaxed and passively sank for a time before jetting again.

TEMPERATURE EFFECTS

Earlier experiments showed that *I. illecebrosus* eggs will not develop at temperatures below about 13°C (O'Dor *et al.,* 1982), and the present experiments show that they develop at temperatures at least as high as 26°C. In fact,

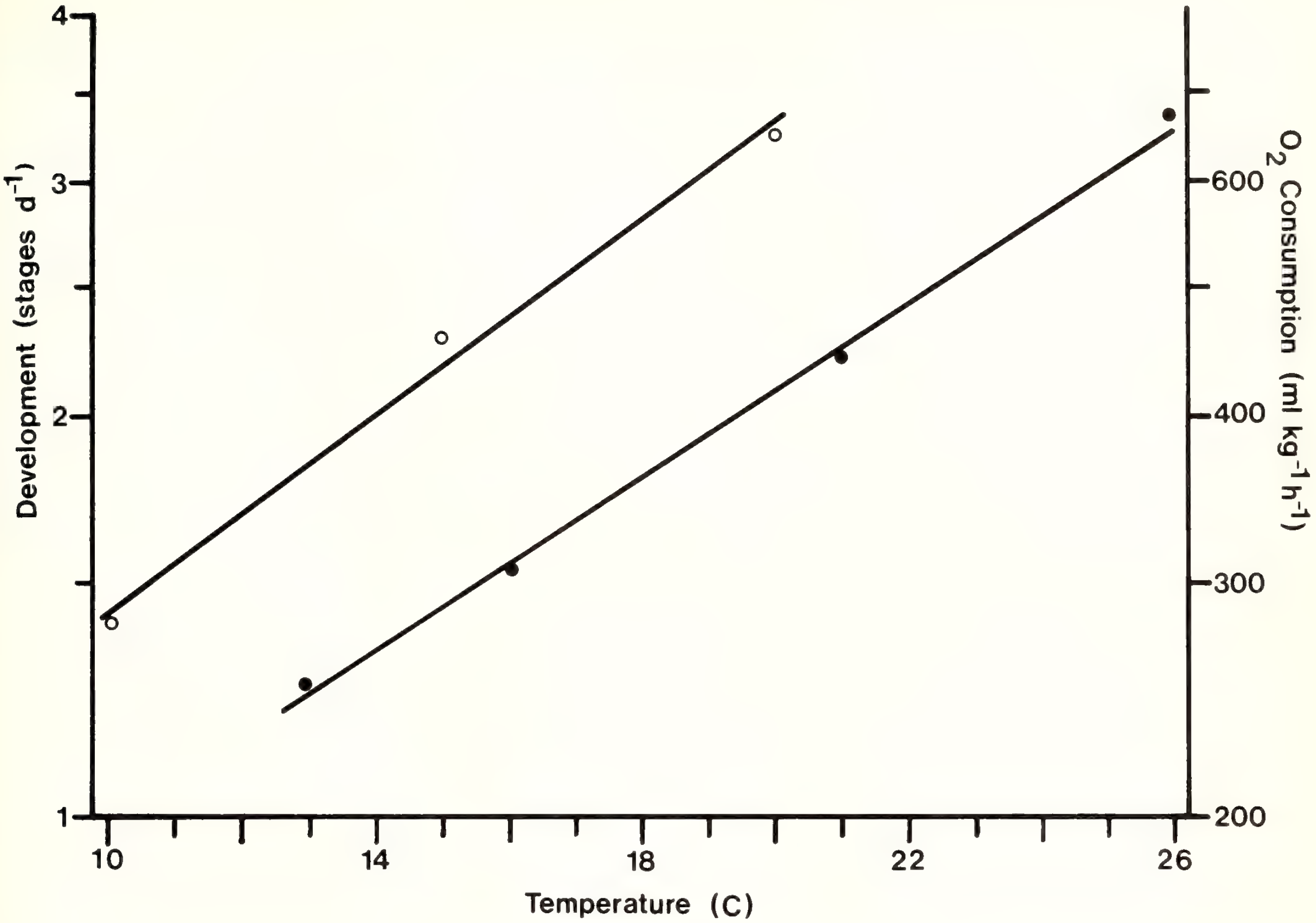

Fig. 1. Temperature effects on development and metabolic rates in newly-hatched squid. Development rates (filled circles) are for *I. illecebrosus* and are given in stages per day (20 stages divided by the number of days to hatching; staging and some data from O'Dor *et al.*, 1982). Oxygen consumptions (open circles) are for *L. opalescens* from Hurley (1976). Lines are regressions of the form $R = B(A)^T$. For development, A is 1.0782 (equal to a Q_{10} of 2.12), B is 0.460 and r is 0.9995. For metabolic rate, A is 1.0879 (equal to a Q_{10} of 2.32), B is 123.7 and r is 0.995.

they appear to do better at these higher temperatures. The number of viable hatchlings from the egg mass at 26°C was higher than from any mass observed to date, and they appeared to be more fully developed at hatching. The buccal mass was fully formed and operational, for example, which was typically seen only several days post-hatch in earlier experiments. Records of earlier hatchlings are not precise enough to be sure whether there is really a better coordination of development of all systems at the higher temperatures or whether there was simply a higher proportion of premature hatching at the lower temperatures. In most egg masses at lower temperatures, a fungus develops in the gel after about a week, and as the gel collapses the expanded chorions of the later stages (O'Dor *et al.*, 1982) are more easily ruptured causing premature hatching.

Whether high temperatures ultimately produce more viable squid depends upon several factors. Premature hatching is one, but if the metabolic rate increases faster than the development rate, high temperatures could produce well-formed, fully developed hatchlings which would, however, lack the yolk reserves to sustain them until they begin to feed. Figure 1 shows the development rate (R_d) over the entire range of temperatures (T), and compares this effect to the change in metabolic rate (R_m) seen in hatchling *L. opalescens* (Hurley, 1976). R_d is calculated in stages per day based on the day the first swimming stage XX hatchlings appeared: 6, 9, 13 and 16 days at 26, 21, 16 and 13°C, respectively (O'Dor *et al.*, 1982). A regression of rate against log temperature gives the following relation when back-transformed:

$$R = B(A)^T$$

For development, back-transformed regression coefficients A and B are 1.0782 and 0.46, respectively; this means the time to hatch is approximately halved by a 10°C rise in temperature and that the development rate has a Q_{10} of 2.1 (1.0782^{10}). For metabolic rate, A is 1.0879 and B is 123.7 giving a Q_{10} of 2.3. Thus, both development and metabolic rates increase similarly with temperature, and there is no major

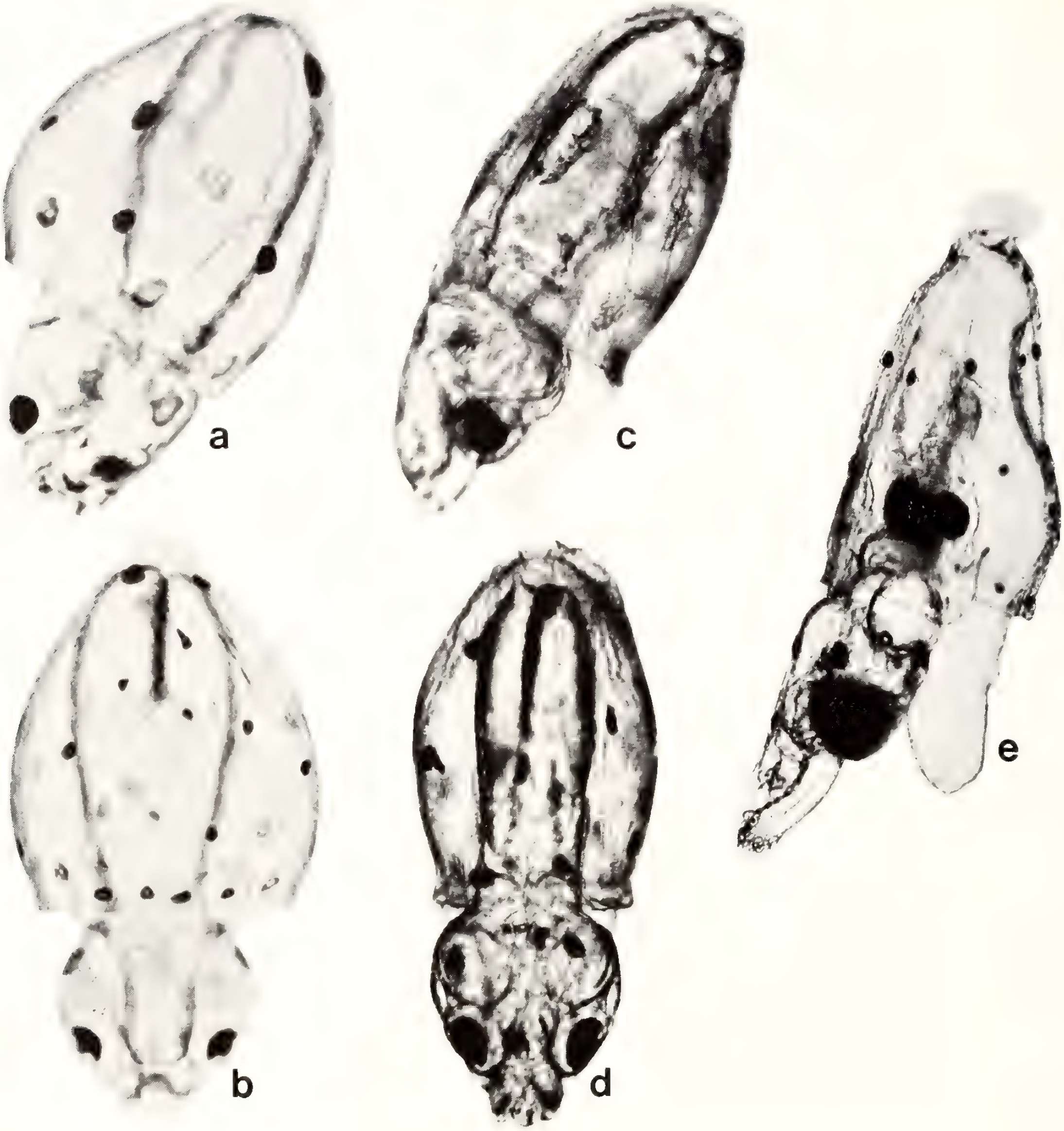

Fig. 2. *Illex illecebrosus* embryo and hatchling photographs used to calculate yolk volume. a) and b) are top and side views of Stage XVII embryos. c) and d) are recently hatched Stage XX embroys. e) is one of the most advanced hatchlings seen to date seven days post-hatching. Its yolk reserve is nearly developed, and it is near starvation.

disadvantage to development at high temperature.

YOLK ENERGY PARTITIONING

Until a newly hatched animal begins to feed, the yolk reserves must meet three requirements: 1) material for further development, 2) energy to meet the demands of standard metabolism and 3) energy for activity. This report attempts to estimate the relative importance of each of these under various natural regimes of temperature and activity and to predict the maximum time available for hatchlings to find and learn to capture food.

The only direct measure of energy consumption available for *I. illecebrosus* hatchlings is the rate of yolk utilization. The precocious hatchlings in Figure 2 a to d were kept at 15°C and photographed 2 days apart at stages XVII and XX of development as indicated. The photographs showing the internal yolk sac were diagrammed and yolk volumes determined as described in Materials and Methods. Assuming a density of 1.036 g cm^{-3} (slightly greater than Aquatron seawater), the weights of yolk at stages XVII and XX were estimated at 113 and 87 μg, respectively. If its caloric value is 1.71 Kcal g^{-1} as in *L. opalescens* (Giese, 1969), the yolk consumed contained 0.045 cal and at stage XX a hatchling would contain 0.148 cal in yolk. After about 7 days at this temperature a hatchling would be devoid of yolk and would starve (Fig. 2e) unless feeding had commenced. Extrapolating from the rate for adults given in Materials and Methods predicts a standard metabolic rate of 0.0050 cal d^{-1} for a 150 μg embryo. When this is deducted it leaves 0.017 cal d^{-1} for growth of developing tissues. The balance is similar in the hatchlings; activity raises the routine metabolic rate to 0.0055 (see Table 1) which accounts for 0.037 cal in 7 days, leaving 0.016 cal d^{-1} for development.

Table 1. Estimates of total metabolism and survival times for *I. illecebrosus* hatchlings at various temperatures and activity levels.

Velocity (mm s^{-1})	Hovering	10	26
Active Metabolism (cal d^{-1})	0.00007	0.00053	0.0048
Standard Metabolism (cal d^{-1})	Total Metabolism(cal d^{-1})/Survival Time(d)		
0.0033 at 10ºC	0.0034 12	0.0038 11	0.0081 5
0.0050 at 15ºC	0.0051 8	0.0055 7	0.0098 4
0.0065 at 18ºC	0.0066 6	0.0070 6	0.0113 3
0.0127 at 26ºC	0.0128 3	0.0132 3	0.0175 2

Table 1 gives the standard metabolic rates at various temperatures, based on a Q_{10} of 2.3, and the calculated costs of swimming at maximum and routine speeds and of hovering. The value for hovering was estimated from the average upward velocity (6.2 mm s^{-1}) and the fraction of each cycle spent moving up (40%). In the matrix of the table, total metabolic rates and estimated survival times under each condition are given. The survival times assume that the same amount of yolk always goes to development, which is reasonable where the temperature effect on standard metabolic rate predominates, since development rate increases in parallel, but may lead to underestimation at high activity where yolk might be used for energy before development could occur.

DISCUSSION

COMPARISON WITH OTHER SQUID

This report brings together all the data available on hatchling *I. illecebrosus* energetics, but, given the rather meager data base, it seems desirable to have some verification of the approach before discussing the conclusions and implications. Table 2 summarizes some basic data for *I. illecebrosus* and compares them to similar values for *L. opalescens* and *L. vulgaris* hatchlings, giving the sources of data and indicating how estimates were made. The three data sets are complimentary, each having some directly measured data that the others lack; thus calculated values can be tested. The difference between standard and routine metabolic rates for *L. opalescens* is 20 cal g^{-1}d^{-1} which would allow a routine speed of 25 mm s^{-1}. This is 2.5 times the speed observed for *I. illecebrosus*, and since *L. opalescens* is 2.5 times longer, this suggests that "cruising" speed scales directly with length as is found in fish. The calculated speed is comparable to the observed speeds of *L. vulgaris* hatchlings.

Table 2. Summary of data on locomotion and energetics in hatchling squid of three species at 15ºC. Values in parentheses are new estimates for the table; unless indicated by a letter, other data are either original observations, calculations from the text or direct unit conversions. Reference sources are: a) Fields, 1966. b) Hurley, 1976. c) Mangold-Wirz, 1963. d) O'Dor, 1982. e) Packard, 1969. f) Webber and O'Dor, 1985.

EGGS	*Illex illecebrosus*	*Loligo opalescens*	*Loligo vulgaris*
Size (mm)	0.9x0.6	2.3x1.5a	2.0x1.5c
Weight (mg)	0.21	3.0a	2.6c
HATCHLINGS			
Weight (mg)	0.15	3.4b	3.6e
Total length (mm)	1.8	4.4b	6.0e
Maximum velocity (mm s^{-1})	50	(130)	160e
Routine velocity (mm s^{-1})	10	(25)	30e
Standard metabolism			
(m10$_3$kg^{-1}h^{-1})	303f	257d	—
(cal^{2}g^{-1}d^{-1})	33	28	—
Routine metabolism			
(cal g^{-1}d^{-1})	38	48b	—
(cal d^{-1})	0.006	0.16	—
Yolk content (cal)	0.148	3.05a	—
Yolk available (cal)	0.039	(0.81)	—
Survival time (d)	7	5	—

The predicted survival time for starving *L. opalescens* is short, but not unreasonably so. Fields (1965) reports that at 15ºC hatchlings that were apparently not feeding all died in less than 10 days. In any case, the assumption that *L. opalescens* hatchlings use the same proportion of yolk for growth and development as *I. illecebrosus* is probably the least defensible argument in the analysis since *L. opalescens* hatchlings are much more highly developed at hatching and essentially able to function as miniature adults.

A final observation suggesting that the calculations of the cost of locomotion are reasonable is that a regression of weight on cost of transport for *L. opalescens* and *I. illecebrosus* in the range of 40 to 400 g predicts values for the hatchlings of both species differing by less than 10% from the values calculated from drag estimates.

DISTRIBUTIONAL IMPLICATIONS

The observations on *I. illecebrosus* seem to raise a dilemma. Egg development proceeds most efficiently at temperatures as high as 26ºC, but hatchlings have fewer than three days to find food and learn to capture it at these temperatures. Since learning may require some time

(Hurley, 1976), this could be a serious problem in relatively oligotrophic waters where such temperatures exist in winter when the major stocks of *I. illecebrosus* are spawned. The requirement for warm temperatures is consistent with recent observations of captive squid spawning nearly neutrally buoyant egg masses while swimming (O'Dor and Balch, 1985); thus allowing them to spawn in the warm surface waters and the egg masses to remain above the thermocline long enough for the eggs to develop. But what happens to the hatchlings? Since the hatchlings can swim vertically at reasonable speeds and costs, the trade-off between the rate of yolk utilization and the period to attain feeding success may be optimized by vertical migrations. This tactic has long been proposed for zooplankters in general (McLaren, 1963). Although it has not been possible to demonstrate negative or positive phototaxis in captive hatchlings, in nature there is some evidence that vertical migrations of early juveniles may occur (O'Dor, 1983).

There may be several advantages to such behaviour for the squid. If the present analysis is correct hatchlings could, for example, sink over 200 m in 12 h and ascend the same distance in 6 h at their typical speed with a cost of less than 0.0003 cal d^{-1}. The standard metabolic rate at 26ºC is so high that the energy saved in 20 min. at 10ºC or 30 min. at 18ºC would fuel the trip. The actual rate of ascent or descent may be determined by the need to stay with their prey; they are easily able to match the vertical migration rates of most other zooplankters (Hardy and Bainbridge, 1954; Mileikovsky, 1973). Such vertical movement would be particularly important if the Gulf Stream plays a major role in distributing *I. illecebrosus* hatchlings (Trites, 1983; O'Dor and Balch, 1985). The warm Gulf Stream provides good conditions for eggs and would carry them toward rich upwelling areas along the northern edge of the Stream. Descent beneath the Stream would not only move hatchlings to lower temperatures but also dramatically change their horizontal velocity, providing them with some control over their distribution. There is even some evidence to suggest that it would put them directly into the source of water moving into the mixing zone where food is most plentiful (Yoder *et al.,* 1981). Such behaviours are not yet documented and it is unclear what cues the squid might use to regulate them, but, as Trites (1983) has shown, small changes in the position of animals in the Stream can have dramatic effects on their eventual distribution. With the swimming abilities shown here the hatchlings may be less at the mercy of the sea than expected.

ACKNOWLEDGEMENTS

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LARVAL DEVELOPMENT OF *CORBICULA FLUMINEA* (MÜLLER) (BIVALVIA: CORBICULACEA): AN APPRAISAL OF ITS HETEROCHRONY

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ABSTRACT

Populations of *Corbicula fluminea* (Müller) in intake bays of Arkansas Nuclear One at Russellville, Arkansas were subjected to a continuing 2½ year study of their gametogenic and ontogenetic processes. Videomicroscopy was especially helpful in working out ontogenetic details, though conventional techniques of microscopic serial sections and scanning electron microscopy (SEM) were also used. In this proto-oogamous species it was found that spermatogenesis is synchronously stimulated by temperature rise in the spring and asynchronously stimulated by temperature decline in the fall. Spermatogenesis, in turn, "times" the process of fertilization and ontogeny. *Corbicula fluminea* seasonally develops many thousands of embryos that characteristically differentiate into blastulae, gastrulae, trochophores, veligers, pediveligers and early and late, straight-hinged juveniles. The fall reproductive pulse lasts about 14 days longer than the spring pulse and fall is the only time that evidence of self-fertilization has been gathered. Neither the trochophores nor the veligers appear to be well adapted for a freshwater, planktonic habit. Late pediveligers and early to late juveniles are the stages of development usually shed from the parent clam. Once released from the marsupial gill into the lotic environment, the straight-hinged juvenile grows into an umbonal juvenile at about 500 μm. About three months were required for development of a straight-hinged juvenile into an umbonal juvenile, in laboratory culture. When the shell valves of the umbonal juvenile attain a length of about 1 mm, a byssus is developed. Chronicity of ontogeny is compared with that of certain marine bivalves and with indigenous freshwater corbiculacean relatives of *Corbicula fluminea,* the pill clams and fingernail clams (Pisidiidae). We argue that heterochrony, in the phyletic, evolutionary sense in which it was used by De Beer, very likely accounts for much of the current "success" of *Corbicula fluminea* in the United States.

During a study of the biota of the Arkansas River in Arkansas, in 1974-75, it was found that juvenile *Corbicula fluminea* were the most abundant and widely distributed organisms, by far, in the benthic communities of the 672-kilometers-long study reach (Kraemer, 1976). Ponar grab samples obtained in the study contained thousands of tiny (1-4mm long) clams. Many of the clams were removed with their byssal thread still intact and adhering to sand grains from the substratum (Kraemer, 1979). Sinclair and Isom (1963) had found the veligers of the clams to be "short-term planktotrophic, non-swimming" larvae, which were discharged from the gravid clams into the surrounding water. The only developmental stage which appeared in our samples, however, was the well-differentiated juvenile.

Another finding which emerged from the 1974-75 study was that upstream populations of juvenile *C. fluminea* showed some evidence of recruiting to the downstream populations in successive seasonal sampling series. Though the point was not emphasized at the time, some of the figures (Kraemer, 1979, Figs. 4,5,6) provide the basis for such an interpretation. It seemed that most of the young shed into the environment were juveniles. The juveniles differentiated a byssal thread following their release into the stream and tended to remain close by. Over a period of several months, however, juvenile *C. fluminea* could be transported downstream, perhaps along with sand grains to which their byssus attached, to populate the downstream benthos.

A "clam clog" of the service water system of Arkansas Nuclear One, located on the Arkansas River near Russellville, Arkansas, forced the costly shutdown of the facility in the fall of 1980. The present study grew out of the urgent need for a clear understanding of the details of the reproduction and developmental cycle of *C. fluminea* in the intake bays at Arkansas Nuclear One. From the spring of 1982 to the fall of 1984, populations of *C. fluminea* were subjected to continuing analysis of their gametogenic and ontogenetic

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processes.

Earlier studies on the freshwater corbiculacean relatives of *C. fluminea*, the Pisdiidae (pill clams and fingernail clams), such as those by Heard (1977) and Mackie, *et al.* (1974a,b) afforded a basis of comparison with emerging details on reproduction and development in *C. fluminea*. Kraemer and Lott, (1977), Kraemer (1978, 1979a, 1979b, 1984, in press) and Kraemer et al. (in press) had worked out a series of details, including the fact that *C. fluminea*, unlike the Pisidiidae, is proto-oogamous in its development. Morton (1982) reviewed characteristics of reproduction in *C.* cf. *fluminalis* from the Pearl River near Canton, China, noting that *C.* cf. *fluminalis* (ibid, p. 18) shows ". . . a general trend towards protogynous hermaphroditism" and that *C. fluminea* (in Hong Kong) is ". . . a protandric hermaphrodite." Some details of reproduction and development reported Sinclair and Isom (1963), Aldridge and McMahon (1978) by Eng (1979), and Kraemer (1978, 1979) were evaluated by McMahon (1983) in a comprehensive review of work to date on the ecology of *C. fluminea*.

The present study includes sufficient data to provide the basis for a clear understanding of (1) the role of gametogenesis in the life cycle of *C. fluminea*; (2) the functions of the spring and fall reproductive periods; and (3) many details of embryogenesis. The timing, appearance and behavior of the characteristic embryonic stages of *C. fluminea* presented here, support our hypothesis that the present "success" of *C. fluminea* can be accounted for largely by the heterochronicity of developmental events in its life cycle. Heterochrony is a newly revived idea, rather than a new idea in Biology. Chief among modern explicators of the concept of heterochrony is Stephen Jay Gould. We invite the reader to consider the historical usage of heterochrony as reviewed by Gould (1977), p. 402):

> "HETEROCHRONY 1. According to Haeckel, displacement in time of ontogenetic appearance and development of one organ with respect to another, causing a disruption of the true repetition of phylogeny in ontogeny. The embryonic heart of vertebrates, for example, now appears far earlier in ontogeny than its time of phylogenetic development would warrant.
>
> 2. Cope used the same definition as Haeckel, but viewed heterochrony as support for the biogenetic law. Recapitulation must be defined organ by organ, not in terms of the whole body. The heart may be far more strongly accelerated than other organs, but it is still accelerated, and acceleration is the mechanism of recapitulation.
>
> 3. De Beer defines heterochrony as phyletic change in the onset or timing of development, so that the appearance or rate of development of a feature in a descendant ontogeny is either accelerated or retarded relative to the appearance or rate of development of the same feature in an ancestor's ontogeny."

The reader will note that all of the above definitions concern the matter of *timing* of ontogenetic events and the reasoning that *change in timing* can produce evolutionary change in populations of organisms over generations. The techniques of videomicroscopy and SEM today permit careful monitoring of minute developmental events in the dynamic ecology of molluscan embryos. It is now possible, we think, to extend, amplify and refine the concept of heterochrony, and to advance it as an explanatory principle, for example, for the present ecological position of *C. fluminea* in the U.S. In what follows, the reader is asked to note both the timing and the sequence of developmental events in *C. fluminea*. The reader is also asked to recall that *C. fluminea* characteristically achieves huge biomass in situations of "ecological crunch" (Wiens, 1977), in this instance in U.S. river systems which have been greatly altered by dredging, damming, channelization, and heated effluents, etc.

MATERIALS AND METHODS

From the spring of 1982 through the summer of 1984, specimens of *C. fluminea* were taken from the intake bays at Arkansas Nuclear One near Russellville, Arkansas and shipped to our laboratory in Fayetteville. This was done at monthly intervals in December, January and February, biweekly during early spring and late fall, and twice a week to daily during peak reproductive periods in spring and fall. During this period we periodically collected *C. fluminea* from populations in the White River in Washington County, Arkansas and from the Llano River in Llano County, Texas, for purposes of comparison with the Arkansas River clams.

From May, 1982 to May, 1983, careful dissections of hundreds of clams were carried out in order to obtain an understanding of many aspects of gametogenesis and embryogenesis. Early in the study we realized that ANO personnel were finding embryos in the gills of *C. fluminea* at Russellville often when we were not able to find them in the clams they had sent to Fayetteville. Subsequent checking revealed that the clams, shipped in containers of river water, prematurely shed their embryos during transit. This occurred despite the fact that the shipping distance was less than 160 km, and the clams were cooled during shipment. We found that shipping the clams simply wrapped in moist toweling and cooled, lessened the likelihood of their losing embryos during the journey.

By May of 1984 protocols for evaluation of gametogenic and embryogenic events had been developed and standardized. The protocols provided a consistent method by which details of the developmental process in *C. fluminea* could be worked out. They are purposively quite different from study procedures prescribed by Britton and Morton (1982). Until examined, (usually within 48 hours of shipment) the clams were kept in the cool, moist toweling in which they had been shipped, to prevent shedding of embryos from the marsupial gills. Ten clams from each shipment were systematically treated as follows.

(1) Great care was taken to preserve the integrity of the mantle and the visceral mass during dissection. Forcing the valves slightly apart with a scalpel and holding them thus with one's thumb, an iridectomy scissors was used to cut through the siphons and the posterior adductor muscle (*between* the mantle lobes), and then to cut between the mantle lobes through the anterior adductor muscle. The left mantle lobe was then carefully separated from the left shell valve

and lowered onto the visceral mass. The left shell valve was then removed.

(2) The left mantle lobe was next gently pulled back to expose the gills and the visceral mass. Gills were examined *in situ* with a dissecting microscope for the presence of embryos or larvae. Gills were not removed at this time but were simply folded back to expose the surface of the visceral mass. Using an iridectomy scissors, two incisions were then made. One incision was made parallel and near to the base of the left inner gill. The second incision was cut along the anterior margin of the visceral mass. A jeweler's forceps was used to grip the covering epithelium of the anterodorsal aspect of the visceral mass, near the digestive glands. The epithelium was carefully pulled back, exposing any peripherally located oogenic and spermatogenic follicles.

(3) When present, spermatogenic follicles were located and counted. We found that spermatogenic follicles may be reliably detected when they appear, as a few, whitish, finely granular masses just under the translucent membrane of the visceral mass. Each follicle mass measures about .25mm to .5mm in diameter (Kraemer and Swanson, in preparation).

(4) Spermatogenic follicles were removed from several different locations on the visceral mass. Smears of the tissue were made and examined with an AO 110 Phase-Star compound microscope. Stages of spermatogenesis were identified and characterized as: (a) "Bead." Follicles with few or no mature sperm present. Follicles appear finely granular or bead-like; (b) "SF sperm." No distinctive appearance of the follicle, but many sperm in various developmental stages present; (c) "Ball stage." Follicles typically packed with hundreds of spheres of mature sperm. Kinds and relative proportions of sperm present (round-headed, wide-headed, slender-headed) were determined by means of criteria established earlier (Kraemer and Swanson, in preparation).

(5) Smears were then made of oogenic tissue to determine appearance and size of the oocytes present. In this and all of the foregoing dissections and smear preparations, great care was taken to prevent contamination of the visceral mass by embryos from the marsupial gills.

(6) The visceral mass itself was examined for the presence of embryos, since they had been observed repeatedly by Kraemer (1978) within the oogenic follicles within the visceral mass, in serially sectioned clams. During the course of the current study, several observations of living, early embryos were made from follicular tissues of the visceral mass. Implications of these findings for self-fertilization of *Corbicula fluminea* are discussed further below.

(7) Following detailed dissection of the visceral mass, all four gills were examined. All gills containing embryos (usually just the inner gills) were removed by cutting along their bases with an iridectomy scissors. The gills were placed on a slide in a few drops of conditioned water (i.e. water in which the clams were maintained in the laboratory). Embryos were freed from the marsupial gills by gently teasing the gill tissues apart. The subsequent, mixed sample of embryos was scrutinized to determine kinds of embryonic stages present. All embryos from each gill were counted and categorized if less than 100 were present in each gill, as follows: (a) no embryos present; (b) cleavage, blastula; (c) gastrula; (d) trochophore; (e) veliger; (f) pediveliger; (g) early, straight-hinged juvenile; (h) late, straight-hinged juvenile. If embryos were more numerous, a representative subsample would be similarly counted and categorized. Sometimes the procedure was carried out several times for a clam, when its marsupial gills were charged with thousands of embryos. This was done to ensure adequate representation of the embryonic stages present. Subsample counts from each gill were averaged to determine relative frequency of each developmental stage.

(8) In addition to the foregoing steps routinely carried out on 10 clams per sample, additional clams were examined from each sample in order to obtain further information on developmental sequences, spermatogenesis, follicular development, behavior, state of the different developing tissues and organs, etc.

(9) Many other clams in each sample were used for the purpose of refining our observational techniques with Scanning Electron Micrography, videomicroscopy, phase microscopy, photomicrography and histological techniques.

At the beginning of the study and at intervals throughout the study, careful reference was made to a large series of microscopic serial sections of *C. fluminea* which had been prepared earlier (Kraemer, 1978; Kraemer and Lott, 1977), of a number of clams from the Buffalo River in Arkansas, over the space of 1½ years (1975-1977). During the present study, additional serial sections were prepared of gravid gills of *C. fluminea* containing mostly juvenile clams. All sections were stained with an aniline blue variation of Mallory's Triple Stain (Scmitz, 1967).

A Wild steromicroscope was used in conjunction with a 35 mm Wild MKa 1 camera to visualize and photograph living embryos during the early part of the study. Later a compound AO Microstar microscope fitted with a Panasonic, PK-972 Color Videocamera, and attached to a Panasonic VHS Recorder was used to produce images of living tissues, gametes and embryos on a 19-inch TV monitor. This apparatus provided high-resolution, magnified images of the living embryos and allowed detailed analysis of embryonic behavior as well as of tissue/organ development of the semi-transparent embryos.

Preparation of tissues for SEM involved fixation in 2.0% glutaraldehyde and subsequent processing through cold phosphate buffer solutions and a dehydration series of ethanols. Following critical-point drying with liquid CO_2, the tissues were mounted on studs with silver adhesive solution and coated with 15 nm of gold, using a Polaron SEM Coating Unit, E500. Alternatively, the tissues, following dehydration, were enclosed in small (1 cm^2) packages of Parafilm, immersed in liquid nitrogen, then removed and freeze-cracked by wielding a hammer against a razor blade held on the tissue. These tissues were then mounted, cracked surface up, on the studs before coating. All tissues were then viewed with an ISI-60 Scanning Electron Microscope at 30 Kv and a working distance of 15 nm.

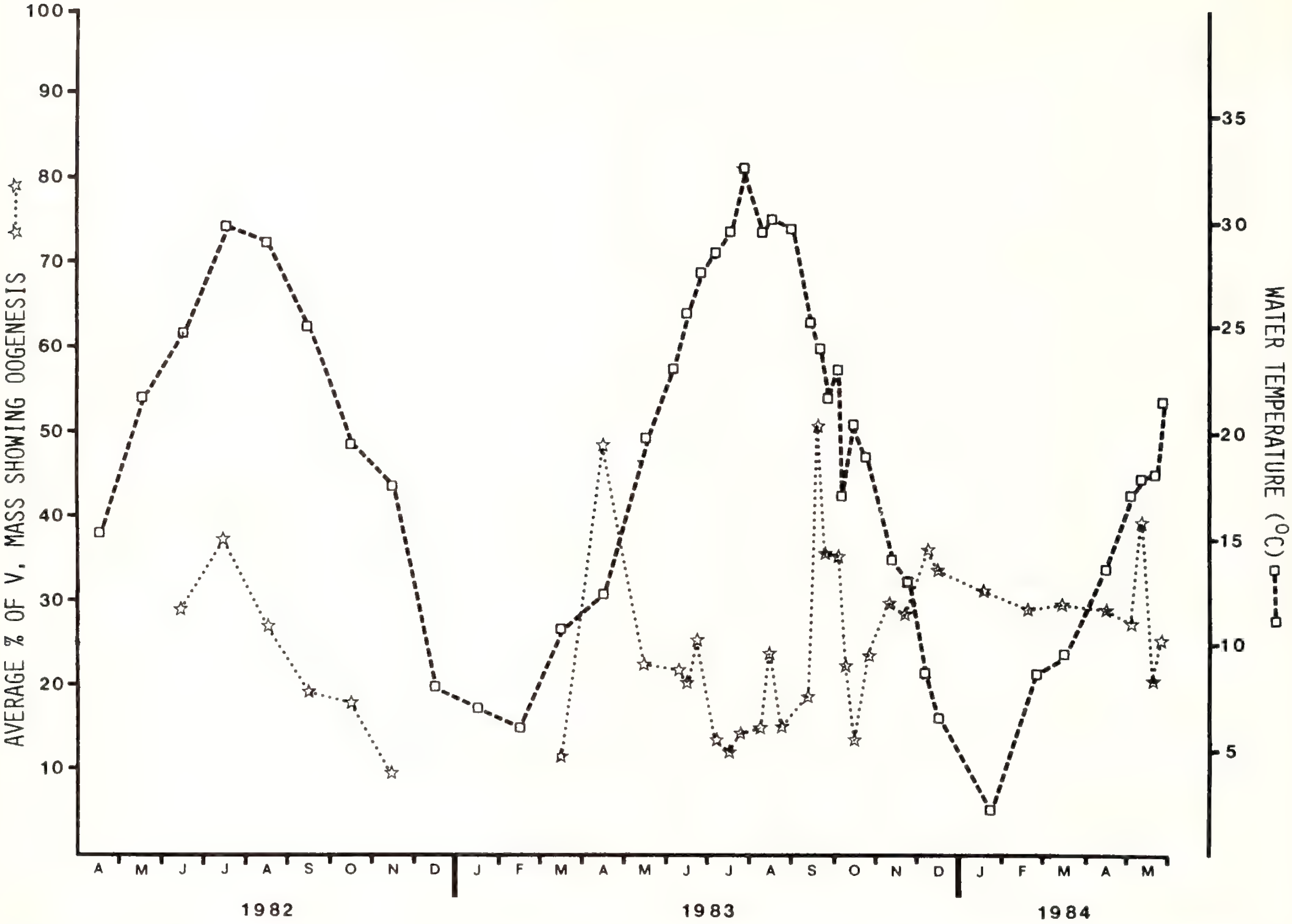

Fig. 1. Average extent of oogenesis in the visceral mass of *C. fluminea* in relation to water temperature in ANO intake bays (Arkansas River) near Russellville, Arkansas.

RESULTS

GAMETOGENIC-ENVIRONMENTAL TIMING

Earlier it was found through microscopic serial section study (Kraemer, 1978) that: (1) Ontogenetically, *C. fluminea* is proto-oogamous, as gametogenesis is initiated when oogenic follicles begin to form in association with the basement membranes of the mucosa of the digestive glands or gut wall. (2) In contrast to the sequence in many bivalves, including the freshwater corbiculacean relatives of *C. fluminea* (family Pisidiidae), the pill clams and fingernail clams, oogenesis seasonally precedes spermatogenesis. (3) It is only when oogenesis is well underway and the oogenic follicles have branched and ramified through the visceral mass, that spermatogenic follicles appear, peripheral to the oogenic follicles.

In the course of this study, which involved careful dissections of fresh tissues of approximately 2000 specimens, the above observations were confirmed and amplified. We now know that in the ontogeny of *C . fluminea*, oogenesis is not only the first form of gametogenesis to occur, but that once begun, it continues throughout almost the entire year in the mature clam. In all months, clams were examined and were found to have all three size classes of ova present in their oogenic follicles. That is, the oogenic follicles contained oocytes measuring $<90\,\mu m$, $\geq 90\,\mu m$, $\geq 140\,\mu m$. There were far fewer of the small-sized oocytes in the oogenic follicles during January, February and March. In April of 1983 and in early May of 1984, there was a marked increase in oogenic follicle development one to two weeks before the appearance of embryos in the gills. In both 1983 and 1984, however, the *onset* of spermatogenic follicle development *preceded* the spurt in oogenic follicle development by 1-4 weeks (Figs. 1,2). Embryogenesis (Fig. 3) followed both.

We now know that *spermatogenesis is definitely a seasonal phenomenon*. We have accumulated evidence indicating rise of spring water temperature to 10°C or more for 7 to 10 days initiated spermatogenesis in 30%, 28% and 42% of the clams in 1982, 1983 and 1984, respectively. Synchronous development of spermatogenic follicles was found in virtually all clams exhibiting spermatogenesis. After spermatogenic follicle development and concomitant spermatogenesis have continued for two to two and a half weeks, and spheres of mature sperm are regularly seen in fresh dissections, spermatogenesis diminishes and the follicles atrophy. After a period of rising water temperature to 17-19ºC for 7-10 days, embryos appear in the gills (Fig. 3). During early summer months there is more variability than there is in the synchronous development of spermatogenic follicles which accompanies water temperature rise in the spring. However, there may be three or four wave-like recurrences of series of developmental stages of *C. fluminea* embryos. It is as though the temperature-induced, spermatogenic spring "pulse" brought about a reverberating series of developmental sequelae in the adult clam. Late in July, apparently in response to sustained high water temperature (29ºC or higher) the reproductive-developmental sequence is interrupted.

The fall reproductive period was initiated in midsummer when the water temperature fell below 29ºC. Evidently because the water temperature fluctuated much more in summer than in the spring, *and* because of metabolic demands already put on energy stores of the clams during spring and summer, onset of spermatogenesis during this period was not synchronous across the population as it had been in the spring. As a consequence of asynchronous spermatogenesis, (more variability of spermatogenic follicle stages present) ensuing embryogenesis was also less synchronozed. In three fall seasons encompassed by this study, the fall reproductive period lasted longer (by an average of 14 days) than the spring pulse (Fig. 3). In both fall and spring several cleavage-to-late-juvenile sequences were seen.

There is some evidence that the fall reproductive pulse is the strongest one: (1) Only in the fall did we make occasional observations of clams with fully gravid inner gills *and* with several water tubes of one or both of the outer gills containing embryos. (2) Our observations of evident self-fertilization were made on clams collected in the fall. Only in the fall did earlier serial section studies (Kraemer, 1978) reveal the presence of *intrafollicular embryos* in the visceral mass. Only in the fall were embryos occasionally seen in fresh

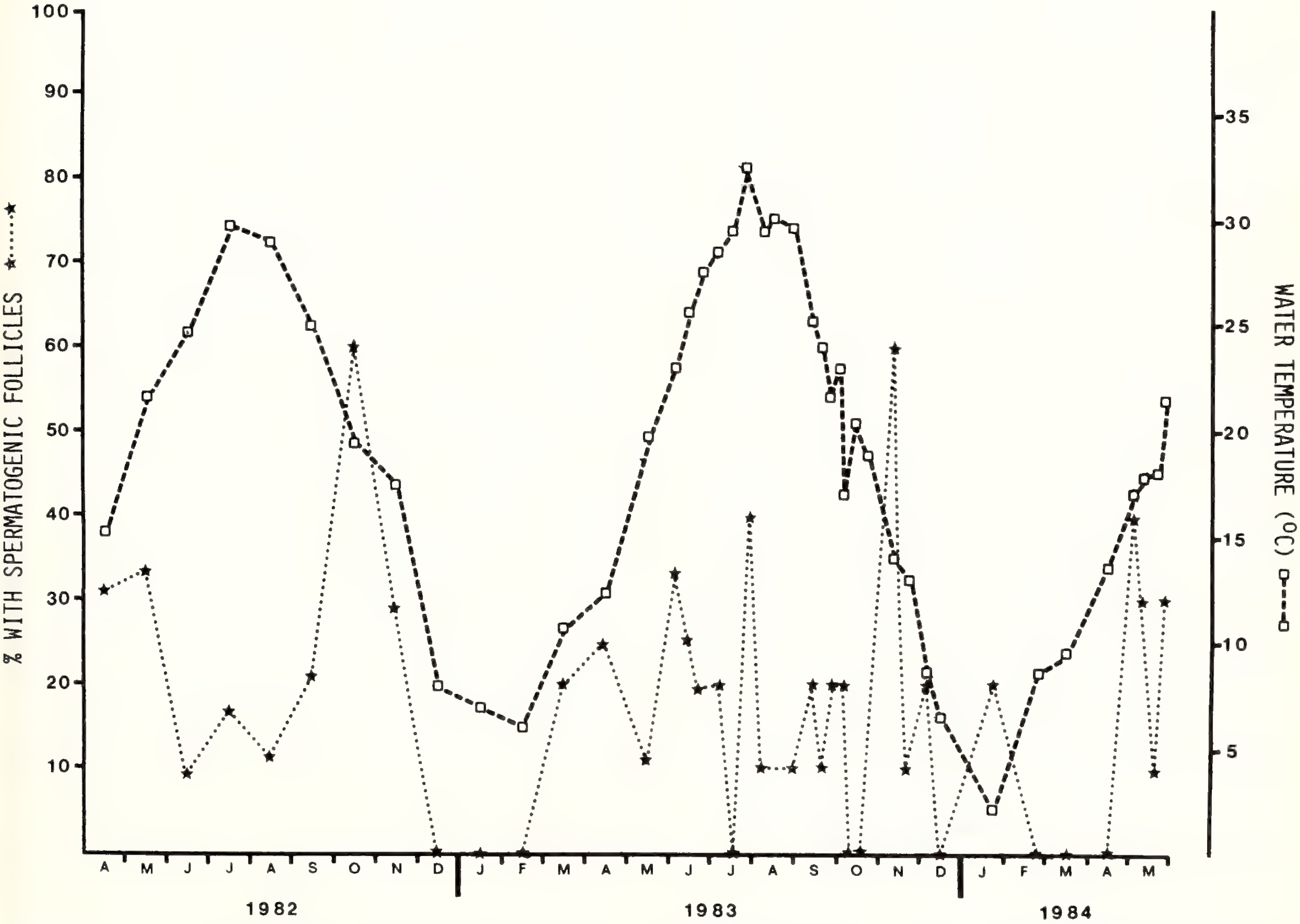

Fig. 2. Percent of *C . fluminea* examined from ANO intake bays (Arkansas River) near Russellville, Arkansas, having spermatogenic follicles, in relation to water temperature. (Note: data point shown for January, 1984 was from shipment which had been held at room temperature for 5 days before dissection.)

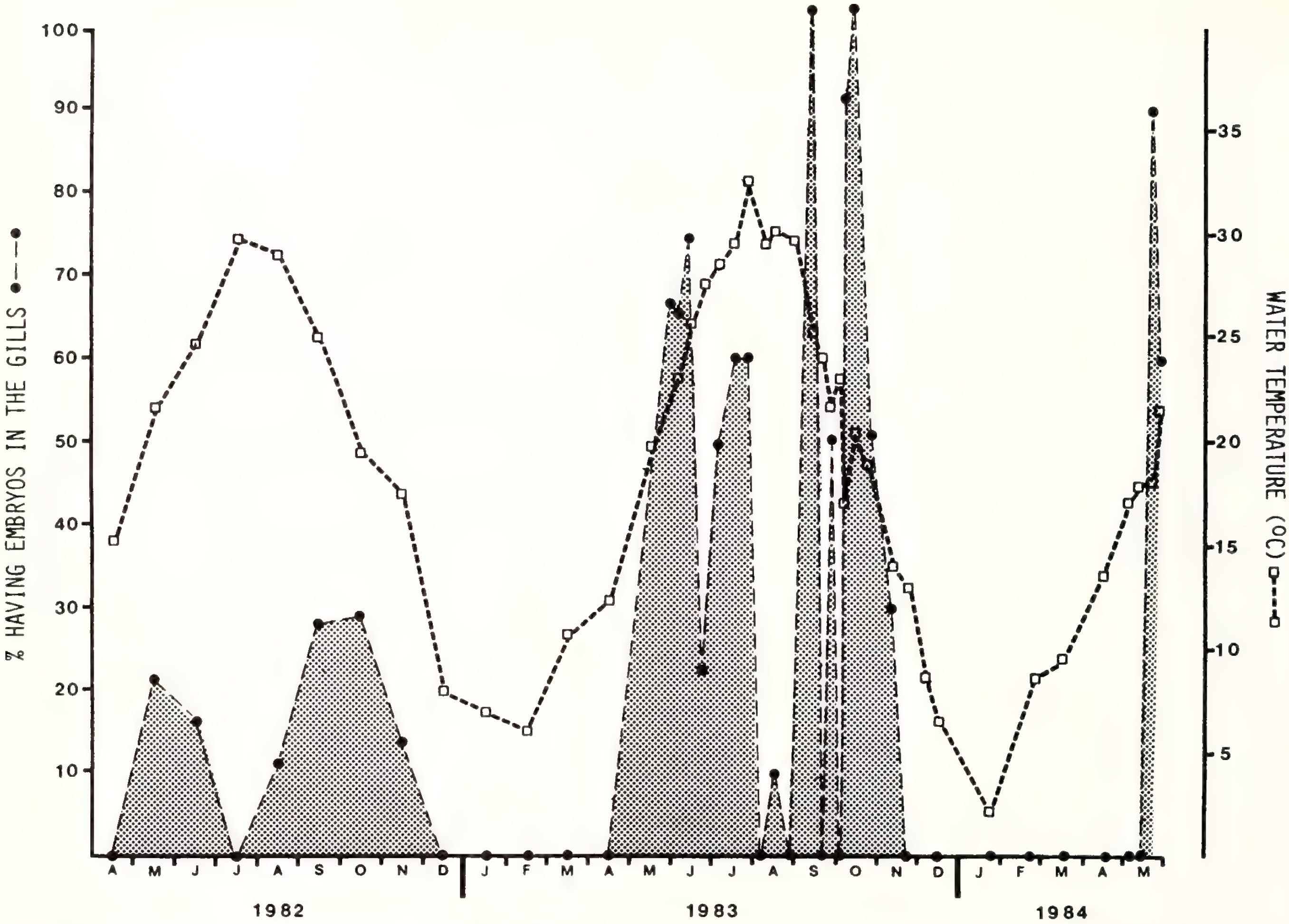

Fig. 3. Percent of *C. fluminea* examined from ANO intake bays (Arkansas River) near Russellville, Arkansas, having embryos in the inner gills, in relation to water temperature.

tissue dissections of the visceral mass. (3) Finally, AP&L personnel have noted that the greatest likelihood of a "clam clog" at ANO in Russellville, has regularly been during the fall.

FERTILIZATION

Earlier studies (Kraemer 1978, 1979, 1984; Kennedy *et al.*, in press; Kraemer, *et al.*, in press) had adduced that *C. fluminea* carries out both self fertilization and cross fertilization. Cross fertilization apparently occurs when spheres of mature sperm make their way out of the gonopores, which are paired and located on either side of the posterior, dorsolateral aspect of the visceral mass (Kraemer, 1978), where the gonopores open into the subrabranchial cavity. Sperm then may be carried to the exterior via the excurrent siphon of the clam and through the water to the siphons of neighboring clams. In this study we repeatedly observed that sperm cells separate from the spheres in the dilute external environment. Sperm thus appear to be transmitted as individual cells. A similar phenomenon regarding the separation of sperm from sperm "morulae" has recently been analyzed in the polychaete, *Arenicola sp.* (Bentley, 1985).

Self fertilization apparently occurs late in the fall reproductive pulse (late September and October in Arkansas) and involves regions of the "follicular ganglia" (Kraemer 1978, 1980, 1984, in press) in areas of contiguity between oogenic and spermatogenic follicles. Serial sections reveal the presence of many embryos there, most being in blastula or gastrula stages. Identification of intrafollicular embryos by means of fresh tissue dissection (as noted in Materials & Methods) showed these also to be usually blastula or gastrula stages.

In this study it was possible to visualize the jelly coat of the oocyte with SEM, along with the yolky cytoplasm and conspicuous nucleus (Fig. 4c,d). Relative size of the oocyte and mature, biflagellate sperm are shown in Fig. 4c,d, though the actual process of sperm penetration was not encountered in our freeze-cracked, SEM preparations. It is possible to identify fertilized eggs in fresh tissue dissections, as they manifest (1) a clearly visible depression in the egg cytoplams, the apparent penetration site (Fig. 5a); and (2) a fertilization membrane and evident loss of the oocyte's gelatinous coat (Fig. 5).

CLEAVAGE, BLASTULA FORMATION

Cleavage in the *C. fluminea* embryo produces coeloblastula comprised of a spherical mass of yolk-laden blastomeres of similar size, which enclose a central cavity. It has been possible to visualize blastulae in serial sections of the visceral mass (evidently a consequence of self-fertilization as noted above). Blastulae have also been dissected from gravid gill chambers (Fig. 6a,b). Blastulae typically measure 175 μm in diameter, and form within 24 hours after fertilization if the water temperature is suitable.

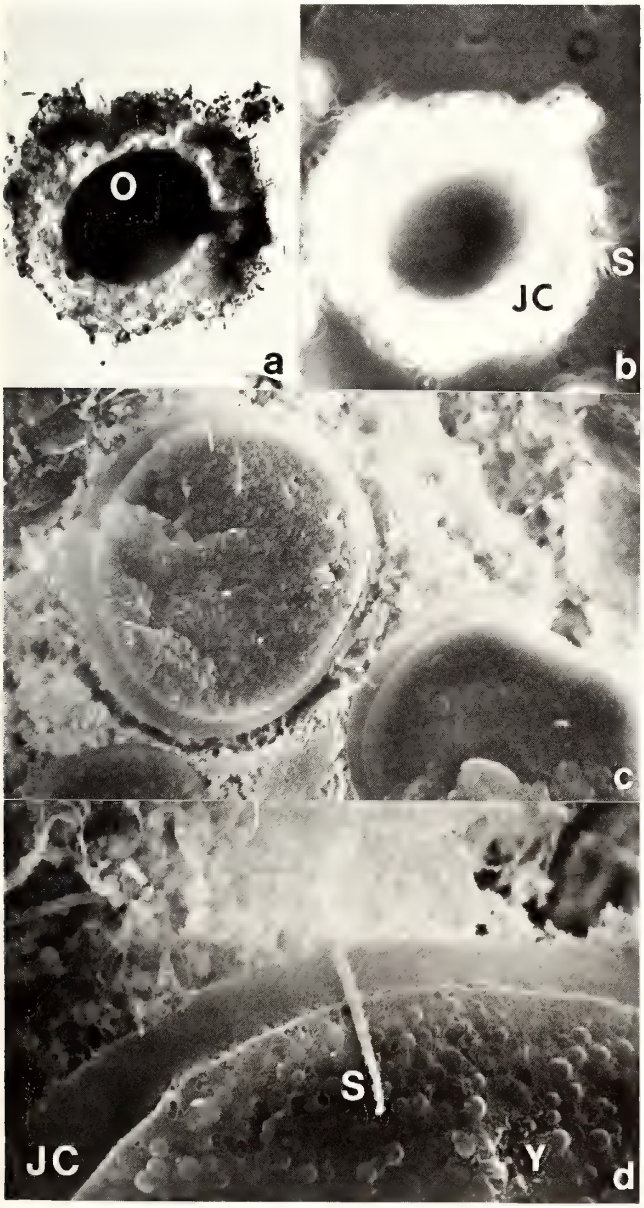

Fig. 4 a,b. Photomicrographs of mature ovum of *Corbicula fluminea* surrounded by a jelly coat containing many embedded sperm. (a) Horizontal field width = 350 μm. (b) Photographed with phase contrast microscopy. Horizontal field width = 400 μm. **c,d.** SEM micrographs of ova, showing freeze-cracked surface of yolky cytoplasm and jelly coat. (c) Horizontal field width = 235 μm. (d) During preparation of the tissue, a mature sperm cell came to lie on the surface of the ovum edge. Horizontal field width = 57 μm. JC, jelly coat; O, ovum; S, sperm; Y, yolk.

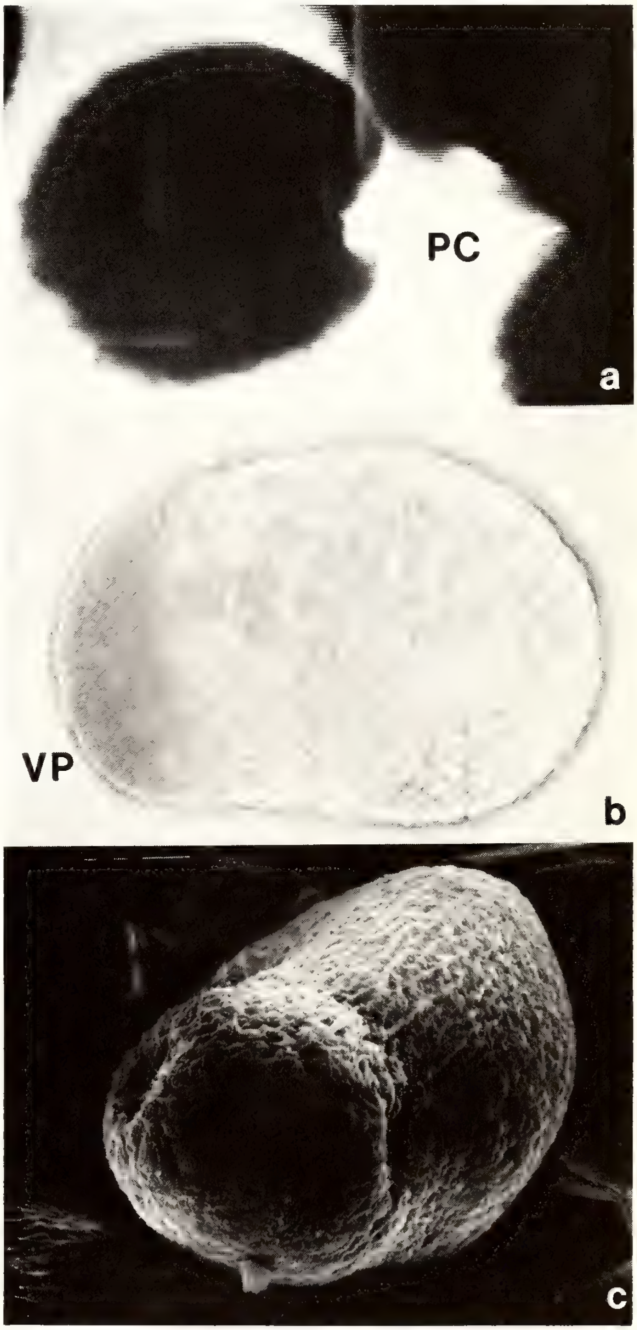

Fig. 5 a-c. Fertilized eggs of *Corbicula fluminea.* (a) Photomicrograph of fertilized eggs, from a videotape, showing evident fertilization or penetration cones, PC. Horizontal field width = 320 μm. (b) Photomicrograph of a fertilized egg as it appears in reflected light, showing more dense aggregation of yolk at the vegetal pole, VP. Horizontal field width = 240 μm. (c) SEM of fertilized egg. Horizontal field width = 230 μm.

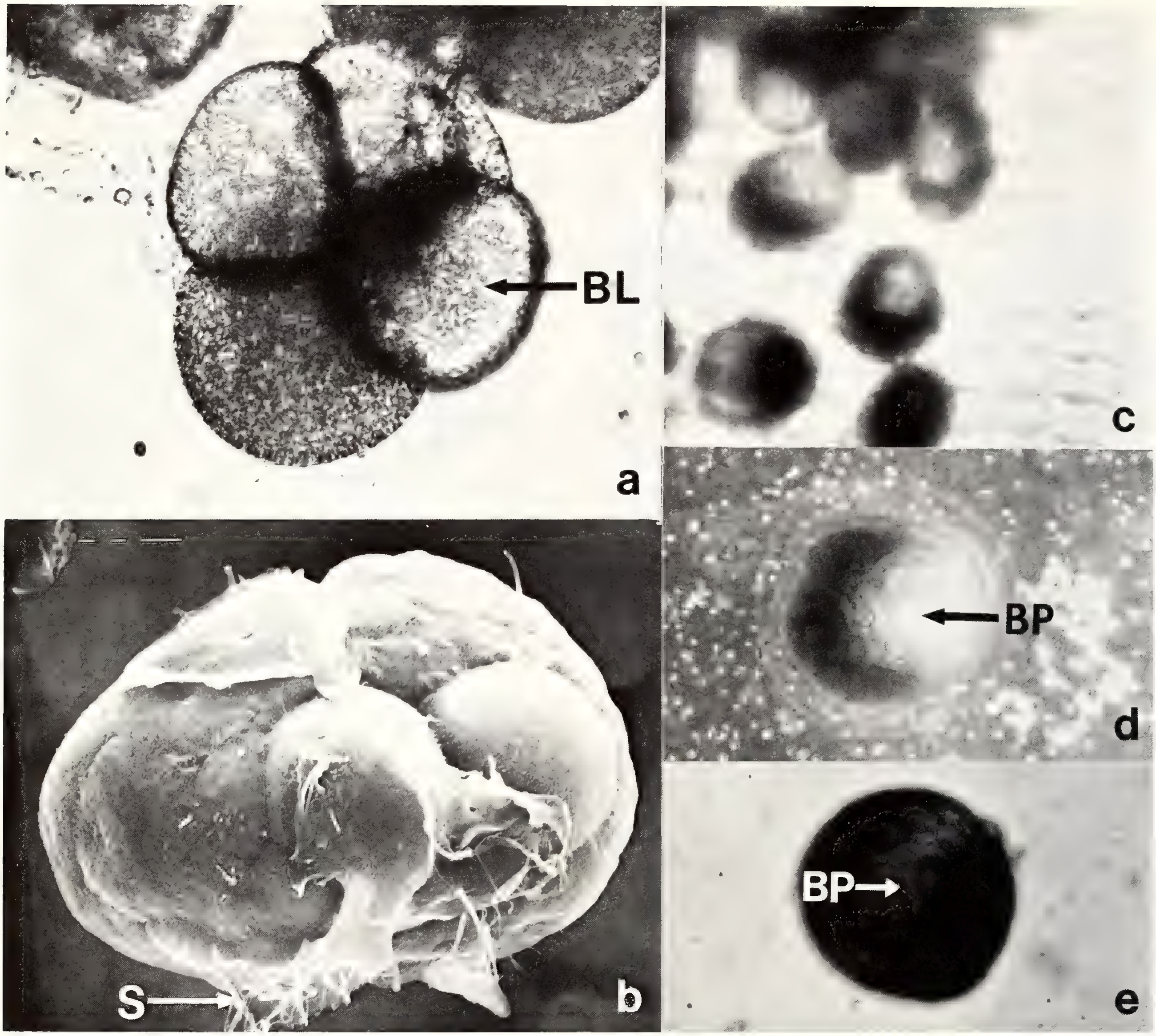

Fig. 6 a-e. Cleavage, blastula and gastrula stages of *Corbicula fluminea.* (a) photomicrograph of cleavage, showing blastomeres, BL. Horizontal field width = 260 μm. (b) SEM of blastula. Horizontal field width = 160 μm. (c) Photomicrograph of gastrulae in marsupial gill. Horizontal field width = 700 μm. (d) Photomicrograph of gastrula, phase contrast. Horizontal field width = 285 μm. (e) Photomicrograph of gastrula. Horizontal field width = 285 μm. BP, blastopore.

GASTRULA FORMATION

Following blastulation, cell proliferation and cell migration produce a gastrula which is bluntly cone-shaped. A large blastopore provides the vegetal pole of the gastrula with an almost flared appearance (Fig. 6c,d,e). Gastrulae appear about 30 hours after fertilization and measure 175-180 μm in diameter.

DEVELOPMENT OF THE TROCHOPHORE

In dissections of fresh tissue of *C. fluminea*, trochophore larvae were frequently seen in the inner, marsupial gills. They could be visualized with SEM, packed into the gill chambers and measuring about 180 μm long. With light microscopy we observed the living trochophores at length as they made their way out of the gill chambers (when artificially freed from gill membranes) and either drifted passively or swam actively there (Fig. 7). Invariably the apical cilia (Scheitelorgan) were "anterior" as the trochophore swam vertically, horizontally or occasionally in a circular path along with other trochophores. When thus observed, the apical cilia of the trochophore are quite mobile and will bend or momentarily retract as the trochophore comes in contact with other larvae or with predators.

For marine bivalves there appears to be some discrepancy in the literature as to which larval stage is a trochophore and which is a veliger. Kume and Dan note (1968, p. 500):

> "No drastic change in body form is involved in the shift from trochophore stage to veliger stage and the boundary drawn between the two stages varies from one investigator to another. The present description (of Kume and Dan) will treat the period lasting until the larval shell becomes prominent as the trochophore stage."

Galtsoff (1965) reports that the marine bivalve, *Crassostrea virginica*, developes distinct valves while still a trochophore, and before the velum appears. In our present study of *C. fluminea*, the trochophores appeared radially symmetrical with light microscopy. With SEM, however, we were able to discern initial development of shell valves during the latter part of the trochophore stage. Like Kume and Dan (1968) and like Waller (1981) for *Ostrea edulis*, we wish to designate the trochophore stage of *C. fluminea* as that period in the development of the clam when it retains an ovoid shape and, with light microscopy, shows no distinct shell valves and no velum.

In the course of this study, trochophores were rarely found in the water surrounding the clams. On a number of occasions it was observed that trochophores released into the water would swell in evident osmotic response. Concomitant behavioral change to a wobbly, attenuated swimming movement, impelled us to conclude that the trochophore larva of *C. fluminea* is not well suited to a free-living, freshwater habitat. This conclusion affirmed that earlier contention (Kraemer, 1979a) that the trochophore does not appear to be the usual distributional larval stage for the species. Just why *C. fluminea* persists in producing a trochophore, a larval stage which *is* the distributional stage for many marine species, will be considered below.

VELIGER LARVA

Observations made throughout several seasons of developmental sequences produced evidence in our study that veliger larvae are regularly developed by *C. fluminea* within the marsupial gills of the parent. Transformation of the trochophore into a veliger is indicated by the development of an asymmetrical profile of the trochophore, when viewed with the light microscope. An asymmetrical aspect results from the growth of the primordia of the shell valves which saddle one side of the "posterior" end of the embryo. Concurrently growth and thickening of the ciliated velum occurs, as it develops from a bilobed outgrowth of the prototroch, just posterior to the Scheitelorgan. The Scheitelorgan persists, and is still tactile and retractile; but the veliger as a whole moves only sluggishly. The velum continues to protrude through the growing shell valves, and indeed cannot be completely withdrawn. Veligers are fully formed from trochophores in about 24-48 hours. Typical length of the veliger measures 190-250 μm (Fig. 8a,b,c).

When veligers were exposed during this study to water surrounding the clams, tissues of the veligers often became

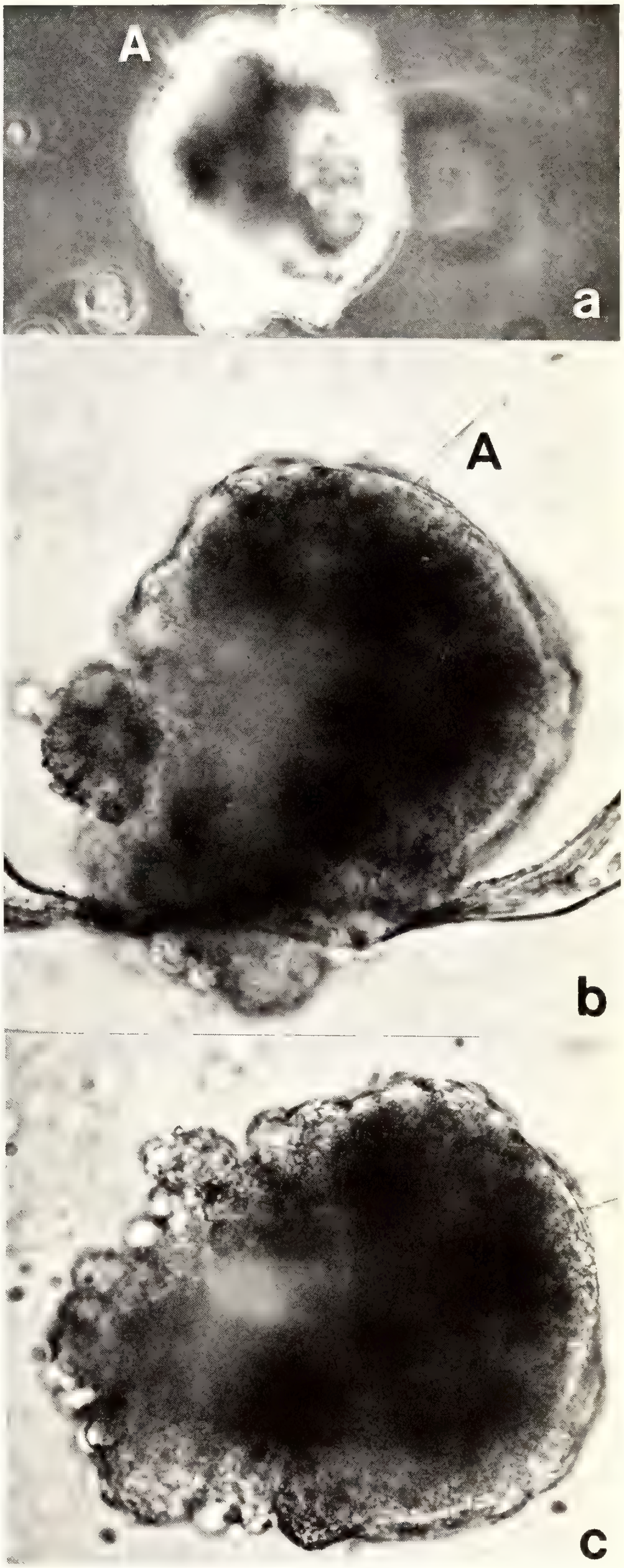

Fig. 7 a-c. Photomicrographs of trochophores of *Corbicula fluminea* from gravid gill. (a) Trochophore photographed with phase contrast. Horizontal field width = 420 μm. (b), (c) Horizontal field width = 205 μm. A, apical cilia (Scheitel-organ).

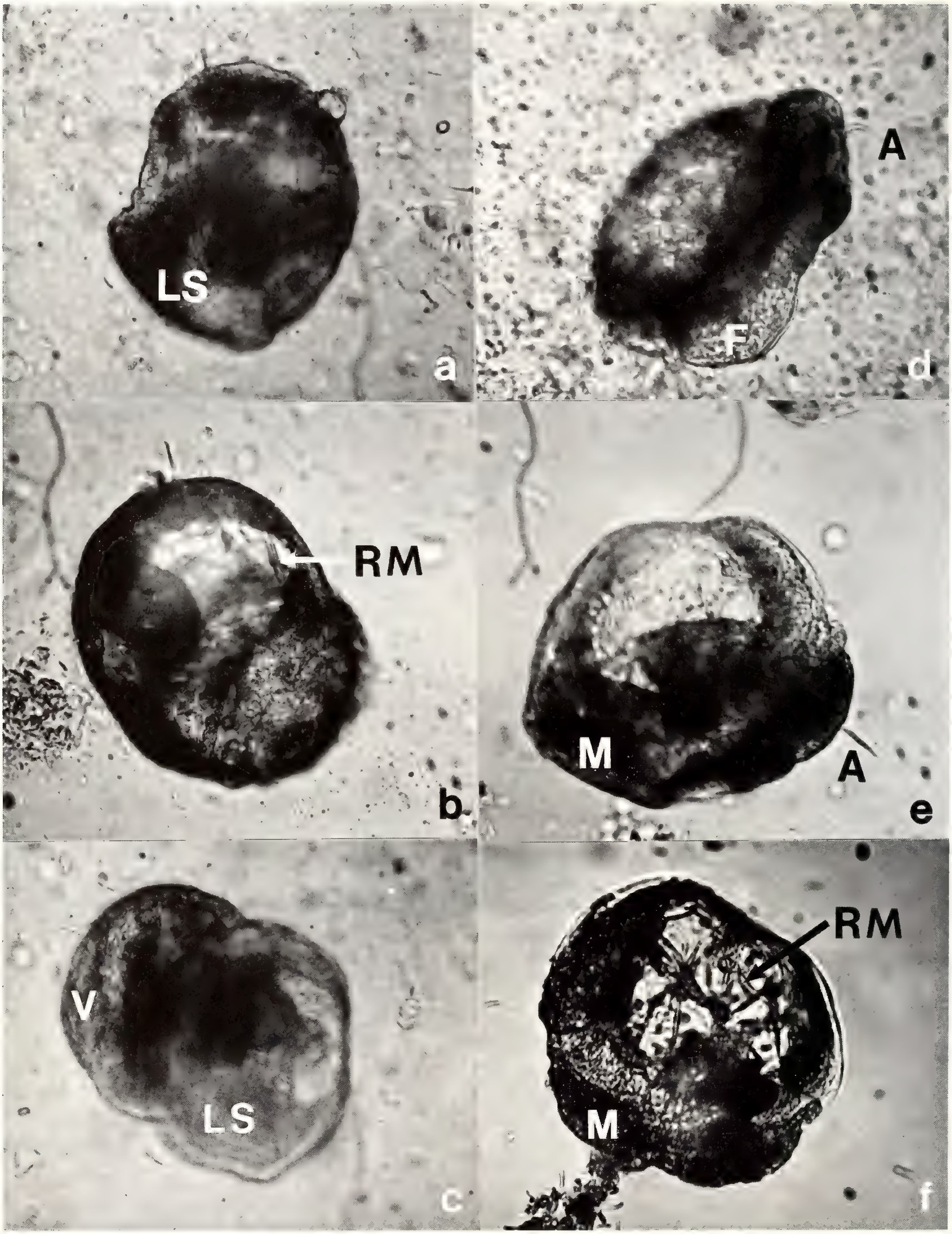

Fig. 8 a-f. Photomicrographs of veligers and early pediveligers of *Corbicula fluminea.* (a), (b), (c) veligers. (b) especially, shows swollen aspect of a veliger in osmotic distress after being exposed to river water. (d), (e), (f) pediveligers. (d) velum and foot extended, mantle retracted. (e) velum extended; mantle extended in posterior region. (f) velum extended; obscuring extended foot. A, apical cilia; F, foot, LS, larval shell valves; RM, velar retractor muscle; V, velum. Horizontal field width = 255 μm.

swollen (Fig. 8a,b). The veliger stage, like trochophore, seems not well suited to a free-living habit in fresh water. It therefore appears unlikely to us that the veliger is a distributional stage for *C. fluminea*.

PEDIVELIGER LARVA

Lengthy observations of living embryos also produced clear evidence of the presence of a pediveliger stage in the ontogeny of *C. fluminea*. The Scheitelorgan persists in this stage. Distinctive characteristics of the developing pediveliger include: (1) The juvenile foot develops immediately posterior to the velum. The enhanced magnification-resolution or our videomicroscopy apparatus enabled us to distinguish the incipient foot from the velum, since the former is a translucent, ciliated, triangular projection of tissue adjacent and posterior to the opaque velum. (2) Larval shell valves grow so that the velum may almost be retracted between them. Subsequent growth of the valves allows complete retraction of the velum, late in the pediveliger stage. The pediveliger stage lasts about 3-5 days. The fully formed pediveliger has straight-hinged valves which measure about 230 μm in length (Fig. 8d,e,f).

While the opaque-appearing velum is still clearly evident and "marked" by the persistent Scheitelorgan, there is another opaque area present which encircles the periphery of the developing animal inside the valves. The latter opaque tissue becomes most evident near the end of the pediveliger stage. The tissue is extensive and bilateral and is especially apparent in the posterior region of the young clam in the early juvenile stage. That it surrounds the differentiating rectum in the region where the siphons and siphonal pocket will eventually develop, is evident from the fact that we have seen fecal material discharged from between the lobes of opaque tissue there (Fig. 9d).

SHEDDING OF THE VELUM AND TRANSITION TO STRAIGHT-HINGED JUVENILE

The veliger shell valves broaden and lengthen during their growth in the pediveliger stage. The velum of the well developed pediveliger is readily withdrawn between the valves by means of the fully differentiated velar retractor muscles (Fig. 8f).

During this study late pediveligers (under pressure from a coverslip) were often observed to extend the velum and to adduct their valves repeatedly or to sustain valve adduction while the velum remained extended. Such behaviors frequently resulted in the casting off of the velum (Fig. 9a). However, there were many observations of the spontaneous shedding of the velum (Fig. 9b), which enabled us to recognize a characteristic, smooth, very distinct convex curve in the distal edge of the visceral mass just at the site where the velum was lost. This "abscission site" can be recognized readily even though the shed velar tissues are gone (Fig. 9c).

It seem inappropriate to use the term, "metamorphosis," for events accompanying shedding of the velum in *C. fluminea*. Nothing comparable to the extensive loss of other larval structures, which coincides with loss of the velum in marine bivalves such as *Crassostrea virginica*, takes place when the velum is shed by *C. fluminea*. Because the velum is removed while the shell valves are still straight-hinged, we have designated the developmental stage in *C. fluminea* which follows velum removal, the straight-hinged juvenile. We are aware that there is no comparable stage in the development of marine bivalves, which retain their velum well through the umbonal stage. Implications of the foregoing events as they relate to the heterochronous development which we have clearly discerned in *C. fluminea*, will be discussed below.

In the transition from pediveliger to the early, straight-hinged juvenile stage, growth of the foot is accompanied by visible change in its form and function, from pointed and inactive to long, sock-shaped and highly mobile. The early juvenile foot is very large and constitutes about one-third of the volume of the animal housed within the valves. There is no significant change in valve dimensions from late pediveliger through early juvenile stages, approximately 230 μm.

THE STRAIGHT-HINGED JUVENILES, EARLY AND LATE

By far the most active developmental stages of *C. fluminea* are the early and late juvenile, straight-hinged stages. With the help of videomicroscopy (described above) it is possible to observe details in the transition of the young clam from its early to late, straight-hinged stages: (1) The gills develop from simple loops attached to the mantle and to the differentiating visceral mass, and then become double loops covered with large, multiple cilia or cirri (Fig. 10c,d,e). The latter, beating like paddles, can be seen sorting particles in the gills. (2) Opaque tissues seen earlier at the posterior and ventral margins of the mantle, gradually disappear. That the former is yolk material we have verified with SEM. (3) The heart develops from a single pulsing chamber to a beating ventricle attached to two membranous auricles. (4) Development of the valve and foot musculature can be followed, as the pedal retractors and protractors which are initially located near the tip of the growing foot, extend dorsally to near the top of the visceral mass at the hinge. (5) The posterior part of the gut and rectum differentiate and become functional, and the production of fecal material can be seen well before the siphons have differentiated. (6) The anterior part of the gut and the style sac differentiate and can be seen to swirl one-celled algae down into the ciliated vortex of the stomach. Some juveniles removed from the marsupial gills had green algae as gut contents, thus indicating that the juvenile clams can feed while they are still in the marsupial gills of the parent. (7) Development of the mantle and the pallial musculature can be monitored and seen to function in the sequence of foot withdrawal, valve adduction, and pallial closure in the juvenile clams. (8) Differentiation of the pedal ganglion and of the statocysts can be clearly observed. With videomicroscopy the statocysts are distinctly seen to be paired and conjoined in the midline. Until the present study, the only other visible evidence of the statocyst organization in *C. fluminea* was from the study of microscopic, serial cross sections by Kraemer (1978a).

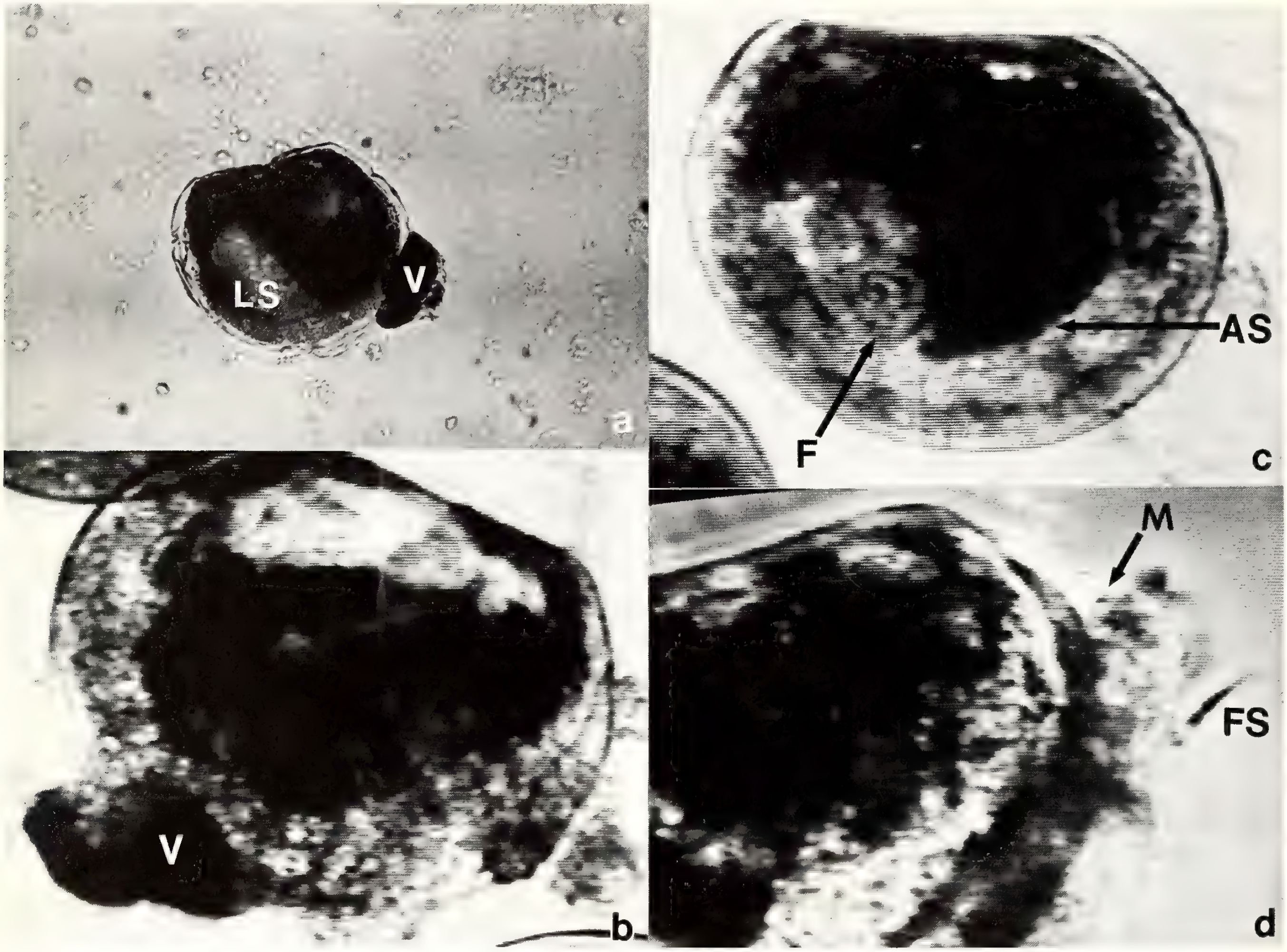

Fig. 9 a-d. Photomicrographs of *Corbicula fluminea* during transition from late pediveliger to early juvenile stages. (a) Late pediveliger shown "casting off" the velum, after repeated adduction of valves was induced by pressure of coverslip on the embryo. Horizontal field width = 570 μm. (b) Late pediveliger shown spontaneously casting off velum. Micrograph from videotape. Horizontal field width = 250 μm. (c) Early juvenile, immediately following casting off of velum, showing "abscission" site from which velum was recently detached. Micrograph from videotape. Horizontal field width = 260 μm. (d) Photomicrograph from videotape of young juvenile showing fecal strand emerging from between distended mantle lobes. Although siphons have not yet formed, posterior region of gut has differentiated and is functioning. Horizontal field width = 230 μm. AS, abscission site; F, foot; FS, fecal strand; LS, larval shell; M, mantle; V, velum.

What has not been appreciated until the present study, is the fact that the statocysts are large (approaching adult size at 15 μm) and well differentiated in the juvenile clams. With videomicroscopy the statocysts can be observed during foot movements. In the early juvenile, the statocysts are located in the distal half of the foot, (Fig. 9c) and in the later juvenile the statocysts are found in the proximal third of the foot (Fig. 10b,c,d). It is apparent that the change in position of the statocysts is due to progressive lengthening and differentiation of the foot. High-power videomicroscopy allowed us to note that the statoliths in both statocysts are also differentiated and move continuously as the juvenile clam's foot moves. The statocysts of *C. fluminea* are much implicated in the movements of the juvenile foot.

In the course of the present study, SEM micrographs of the foot of the juvenile clam revealed a series of 10-12 membranous laminae which comprise the outer surface of the foot (Kraemer, 1984). Examination of serial sections had shown the existence of a "segmental" array of horizontal strands of connective tissue and muscle fibers repeated in the interior of the foot from the distal to the proximal portion of the foot. Videomicroscopy enabled us to see the arrangement of the horizontal "ligaments" in the foot and to appreciate the structural/functional basis for the very active, telescoping movements of the juvenile foot. The locomotor behavior of the juvenile clam does not resemble that of the adult. The juvenile readily swings its foot forward or backward, from side to side in a circular movement, or uses the foot to somersault the rest of its body. The shell valves gape widely, and along with the pallium assist the juvenile clam in clinging to bits of detritus, or in floating in the water column, once it is shed. Some workers have reported finding adult clams floating, alive, in the water column (Bob West, personal communication). Prezant and Chalermwat (1985) have evidence to indicate that the adults may drift on mucus strands in the water column and thereby distribute themselves through the benthos. Our studies on the early developmental stages indicate that the straight-hinged juveniles may also ride water currents to new benthic settlement sites.

Viewing the foregoing developmental stages together, we note that there is substantive change of form in the ontogeny of *C. fluminea* between the trochophore stage and the pediveliger stage, when bilateral symmetry is imposed on the larva and the apical organ becomes the anterior end of the young clam. Changes occurring during the development of a pediveliger to an early, straight-hinged juvenile stage involve differentiation of the foot, pedal ganglion, statocysts and gills, and simple casting off of the velum. Little growth occurs between the pediveliger and early, straight-hinged juvenile stage. Further differentiation *and* shell valve growth (to about 240 μm) characterize the development of the later straight-hinged juvenile stage, where it is lodged in the marsupial gill and after it is shed into the environment (Summary diagram, Fig. 11).

RELEASE OF LARVAE FROM PARENTAL GILLS INTO THE ENVIRONMENT

As mentioned above, a difficulty encountered early in the present study was that shipment of clams in river water resulted in premature shedding of embryos from the parental gills. Another observation made repeatedly was that trochophores and veligers, when exposed to ambient water, would often swell and exhibit stressed behavior. The trochophores and veligers of *C. fluminea* are probably not typically used by these freshwater clams for dispersal of their populations. Early pediveligers, furthermore, exhibit only limited mobility and little coordinated movement. When the larval shell valves are just beginning to develop and the velum is not yet thereby hampered in its movement, the young pediveliger may exhibit some coordinated swimming behavior. As the valves grow, they gradually enclose the velum and behavior of the larva becomes increasingly sluggish, as it swims seldom and awkwardly. Late in the development of the pediveliger when the foot has become quite large, the larva is then capable of active pedal locomotion.

From the late pediveliger stage onward, the larvae are capable of migrating through the parental gill tissues and into the siphonal pocket where contractions of the pallial musculature of the parent clam can eject the young clams. While late pediveligers and early juveniles seem, on the basis of this study, to be the usual embryonic stages relased, it is not uncommon for juveniles to be retained within the marsupial gills well into the late straight-hinged juvenile stage. Water temperature and dissolved oxygen are two significant factors which evidently alter timing of the stage shed. If, as this study indicates, straight-hinged juveniles are capable of feeding while still in the parental gill cavity, an abundant food uptake by the parent clam may keep these juveniles in the gills.

DEVELOPMENT TO THE UMBONAL JUVENILE AND BYSSAL STAGES

In this study it was possible to rear some juveniles to a size of 500 μm. At 500 μm the shell valves of the young clam have developed distinct umbones (Fig. 12). We saw no umbonal juveniles, however, that had developed a byssus. Since the smallest clams in which one of us (Kraemer, 1976, 1979a) had found a byssus were already about 1mm long, it may be that our inability to raise juvenile clams to that size precluded our witnessing the development of the byssus stage. High mortality occurred in our larval cultures when the young clams reached a valve length of 280-300 μm. This high mortality appeared to be correlated with the disappearance of certain remaining "opaque areas" (described above), especially those in the visceral mass near the gut. From examination of juvenile tissues with SEM (Fig. 10), these areas appear to consist of stored yolk material which disappears as it is utilized by the juvenile clam. Thus even though juveniles were observed to feed, mortality may have been caused by insufficient nutriment as embryonic yolk supplies were exhausted. We also conjecture that the byssus may not form unless other environmental conditions are suitable, including the mechanical stimulus of a perceptible current.

SUMMARY AND DISCUSSION

Earlier studies considered some developmental differences which had become generally evident in *C. fluminea*, the Pisdiidae and for marine bivalves. Kraemer and Lott (1977), Kraemer (1978, 1979a,b) and McMahon (1984) remarked on those features and some of their implications. Morton (1982) made some contrasting observations about Asian populations of *C. fluminea* and *C. fluminalis*. McMahon (1984) also reminded us of the comparatively recent appearance of *C. fluminea* in the fossil record, in contrast to the much more lengthy paleontological record of the Pisidiidae in fresh water.

In this paper we have reported findings from 2½ years of continuous detailed study of the reproductive and developmental status of living populations of *C. fluminea* in the intake bays of Arkansas Nuclear One on the Arkansas River near Russellville, and from other "natural" populations in the region (see Materials and Methods). We have found that rising water temperature in the spring and declining water temperature in the fall is the salient environmental change which predictably stimulates the onset of spermatogenesis in *C. fluminea.* We have found that spermatogenesis in turn "times" the rest of the reproductive and developmental sequence. A continuing puzzle, and one certainly deserving of analytical experimental study, is that the environmental stimulus of *falling* water temperature which precedes the autumnal reproductive phase, appears to be a different stimulus than the *rising* water stimulus preceding the spring pulse (Kraemer and Galloway, 1985). The clam's different

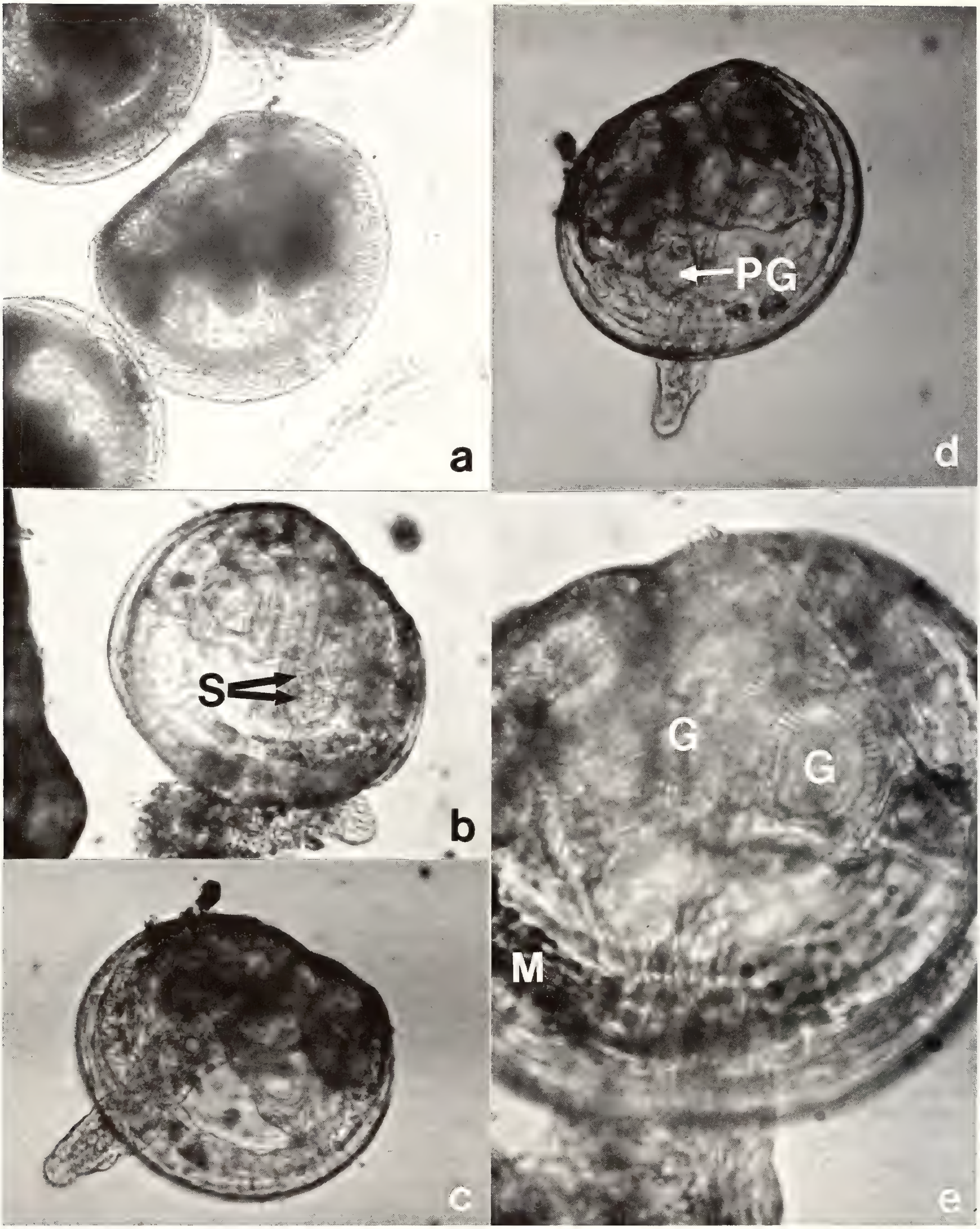

Fig. 10 a-e. Photomicrographs of straight-hinged juveniles. (a) Early, straight-hinged juvenile. (b) Late, straight-hinged juvenile, Oblique view showing, *both* statocysts in the foot. (c), (d) Late, straight-hinged juveniles showing conspicuous, double-looped gills and pedal ganglia. Horizontal field width = 340 μm. (e) Late, straight-hinged juvenile showing double-looped gills with well differentiated cirri. Horizontal field width = 170 μm. G, gill; M, mantle; PG, pedal ganglion; S, statocyst.

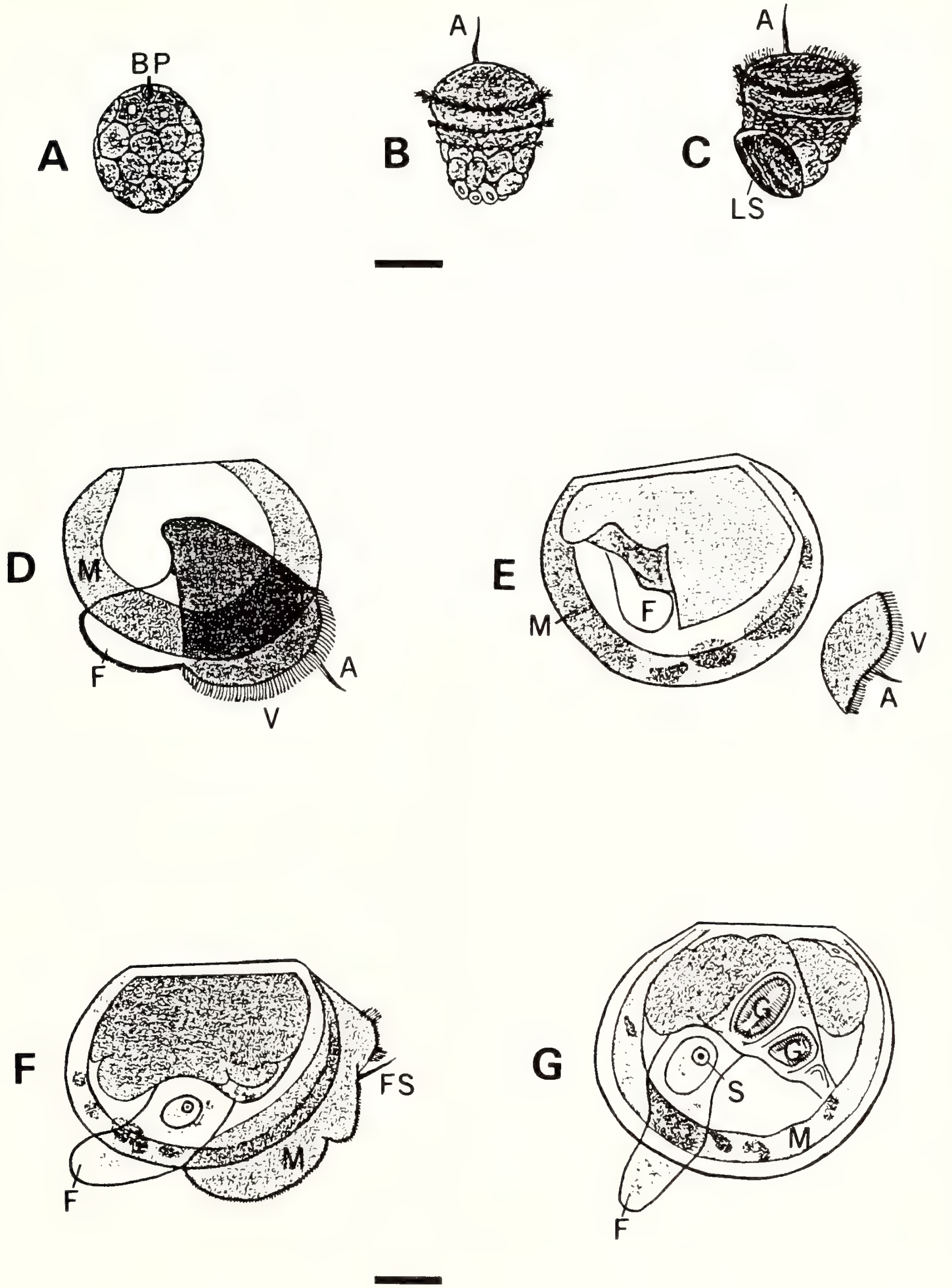

Fig. 11. Summary diagram of developmental stages in *Corbicula fluminea* through the late, straight-hinged juvenile stage. Fertilization, cleavage and blastulation precede A, gastrula stage (shown upside down; B, trochophore; C, veliger; D, pediveliger (anterior end toward right); E, early, straight-hinged juvenile with recently cast off velum, (anterior end toward right); F, early, straight-hinged juvenile (anterior end toward left); G, late, straight-hinged juvenile (anterior end toward left). In this study, embryos were usually shed in the stages from late pediveliger through early and late, straight-hinged juveniles. Two later, post "shedding" stages, the umbonal stage and the byssal stage, are not shown here. Scale bar for a,b,c = 85 μm. Scale bar for d,e,f,g = 55 μm. A, apical cilia; BP, blastopore; F, foot; FS, fecal strand; G, sill; LS, shell; M, mantle; S, statocyst; V, velum; VS, shed velum.

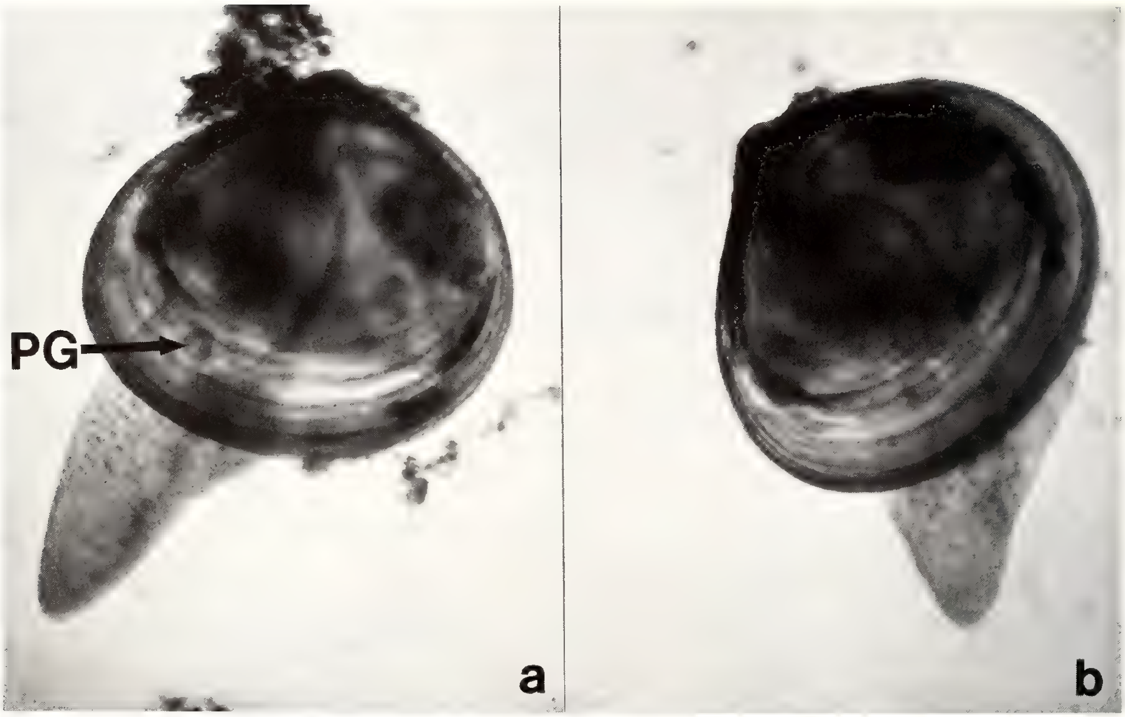

Fig. 12 a,b. Umbonal juveniles of *Corbicula fluminea*. Horizontal field width = 690 μm. PG, pedal ganglion.

reproductive response is surely related to its different metabolic states but may also be affected by the direction and rate of temperature change. Nonetheless, an important result of the present study is the finding that although *C. fluminea* is proto-oogamous, it is *spermatogenesis* that is especially temperature sensitive; and it is spermatogenesis that paces reproductive and developmental processes (see Figs. 2,3). Also, we have found that oogenesis occurs nearly all year long, though it "waxes and wanes" from one season to another.

During the preparation of this paper, we became aware of the ambiguity of the term, "spawning." Spawning has been defined as either the release of gametes or of embryos or young into the environment. *C . fluminea* "spawns" both sperm cells and juveniles. Since some zoologists think of "spawning" as release of gametes only, and others refer to release of young as "spawning" (e.g. Doherty, *et al.,* 1985) we made an effort to avoid confusion, and have eschewed any use of the term.

Though cross fertilization appears to be a typical process for *C. fluminea*, we have found evidence for self fertilization within the gametogenic follicles of the visceral mass, in the fall. Evidence of self-fertilization is summarized in Kraemer, *et al.,* (in press). As noted above, repeated findings were made by Kraemer (1978) on *intrafollicular* embryos in microscopic serial sections of *C. fluminea.* The most parsimonious explanation for these findings is, of course, self-fertilization, i.e., fertilization of mature oöcytes within the oogenic follicles, by mature sperm from the contiguous spermatogenic follicles. Kennedy (1985), though also convinced that self-fertilization occurs in *C. fluminea,* was able to gather only equivocal results from a very painstaking study involving the rearing of *C. fluminea* isolates. The process of self-fertilization obviously requires additional experimental investigation.

We have confirmed that *C. fluminea* regularly produces several sequences of larval stages during each of the two (spring and fall) reproductive seasons. We consistently found the developmental sequence to include: (1) cleavage; (2) blastulae; (3) gastrulae; (4) trochophores; (5) veligers; (6) pediveligers; (7) early straight-hinged juveniles; and (8) late straight-hinged juveniles. (9) Once released into the environment, straight-hinged juveniles eventually grow to a length of 500 μm, in the process differentiating umbonal shell valves; and (10) later producing a byssus when their shell valves approach 1 mm in length. We observed that neither the trochophore stage nor the veliger stage appear well suited to survival in freshwater habitat, but that these stages are typically retained within the gills or mantle cavity surrounding the gills. We continually observed that the young of *C. fluminea* are typically released into the environment in one of the straight-hinged juvenile stages or less often as late pediveligers.

We realize that terms applied to larval stages of marine bivalves both overlap and contrast with terms we have used for ontogenetic events in *C. fluminea.* This is really unavoidable, since our findings clearly show that larval stages in *C. fluminea* actually *do* both overlap and contrast with stages in the development of marine bivalves. Clarification of the embryological terminology used in this paper is offered in Table 1.

Table 1. Comparison of embryonic terms as they apply to an estuarine bivalve, such as *Crassostrea virginica* Gmelin (Galtsoff, 1965) and to *Corbicula fluminea* (Müller) in this paper.

Crassostrea virginica	*Corbicula fluminea*
Fertilization in sea water. Eggs shed into water containing sperm.	Fertilization in marsupial gills or (less often), self-fertilization within gametogenic follicles.
Cleavage.	Cleavage.
Blastula a stereoblastula.	Blastula a coeloblastula.
Gastrula.	Gastrula, cone-shaped with a large blastopore at vegetal pole. 175-180 μm in diameter.
Trochophore, about 60 μm long, with ciliated prototroch as swimming organ. Shell valves prominent with light microscopy.	Trochophore, about 190 μm long, with prototroch and distinct Scheitelorgan, with large, retractile, *motile* apical cilia. Initial development of shell valve observed with SEM.
Veliger, about 70-75 μm long. Velum formed from lateral extensions of prototroch, a *strong swimming organ*.	Veliger, about 190-250 μm long. Velum forms as outgrowths of prototroch around base of Scheitel organ. *Sluggish*. Velar cilia move food particles.
Veliger also called a straight-hinged larva or D-shaped larva. Viewed from dorsal surface, two groups of rectangular teeth are seen on either side of hinge.	Veliger with straight-hinged shell valves. No rectangular teeth lateral to hinge on dorsal surface.
Pediveliger. Larval foot appears.	Pediveliger. Foot appears posterior to velum.
Umbonal veliger, about 300 μm long. Umbones develop on either side of hinge. Well developed velar retractor muscles with striated fibers. Apical organ in center of velum. Gill rudiment present. Pair of statocysts. Pair of larval eyes. Pedal ganglia, pleural ganglia, posterior adductor muscle. Byssal gland opening into mantle at base of foot.	NA
"Metamorphosis." Casting off or disintegration of velum within 48 hours, with "setting" of umbonal veliger. Resorption of foot, degeneration of posterior adductor muscle and larval eyes.	Casting off of velum by straight-hinged pediveliger, to become straight-hinged juvenile, about 230 μm long.
NA	Straight-hinged juvenile is stage typically released from adult into water. Rapid locomotion with juvenile foot. Gills begin to form. Conjoined statocysts, pedal ganglia, esophagus, stomach, intestine, rectum.
NA	Umbonal juvenile stage occurs after 2+ months in substrate (in laboratory culture) when umbones develop on either side of hinge, and clam is 400-500 μm long.
Byssal stage develops in umbonal veliger, described above.	Byssal stage develops in umbonal juvenile. Byssal thread produced from gland and groove in distal portion of foot.

A number of ontogenetic events in reproduction and development of *C. fluminea* seem anomalous when the species is compared with marine and other freshwater bivalved mollusks. Among these are: (1) *C. fluminea* is clearly proto-oogamous, though its indigenous freshwater relatives, the pill clams and fingernail clams (Pisidiidae), in particular, and marine bivalves in general, are protandrous (Fretter and Graham, 1964; Galtsoff, 1964; Raven, 1966; Heard, 1977; Mackie, 1979; Way et al., 1981). (2) In *C. fluminea* development from cleavage to blastula, gastrula, trochophore, veliger, pediveliger, early and even late straight-hinged juveniles *all* occur within the marsupial gill and branchial mantle cavity. The freshwater Pisidiidae, similarly, retain their developing young within the marsupial gill but for a much longer time, until the young are nearly the size of the parent and have begun sexual differentiation (Heard, 1977). Furthermore, the few young which complete development in the parental gills of Pisidiidae never exhibit a trochophore, veliger or pediveliger stage. Okada (19a,b,c) has evaluated the remarkable suppression of larval stages in the Sphaeriidae. In contrast and as shown above, *C. fluminea* has retained the entire sequence of developmental stages in its freshwater habitat, which is characteristic of many *marine* bivalves. In many species of marine bivalves, of course, the gametes are shed and fertilized in the ocean and all ontogenetic stages are free living there. In some marine bivalve species, such as *Ostrea lurida* and *O. edulis*, eggs are fertilized within the marsupial gills and development proceeds in the mantle cavity, so that well developed larvae are released (Galtsoff, 1964). (3) The *rate* of development is rapid in *C. fluminea*, approaching that of marine bivalves (Galtsoff, 1964), and involves the voluminous turnover of relatively small embryos as several ontogenetic sequelae occur with each seasonal reproductive pulse. In contrast, as indicated above, direct development of few young in the Pisidiidae is prolonged in the parental gill marsupia. (4) In *C. fluminea* the released juveniles become umbonal and develop a byssus which is used to anchor the young clam to the river bottom. Byssal stages similarly serve to anchor marine bivalves. In the indigenous freshwater Pisidiidae, however, there is a *marsupial* byssal stage, in which the young develop a "placental" byssus which is used merely to attach the juvenile clam to the wall of the marsupial gill chamber (Mackie, 1978). The foregoing, developmental "timing" differences are summarized in Table 2.

We note that ontogeny of the introduced Asian clam, *Corbicula fluminea*, when compared with the ontogeny of its indigenous freshwater relatives, the corbiculacean pill clams and fingernail clams (Pisidiidae) *and* with the ontogeny of many marine bivalves, exhibits significant developmental "timing" differences. *C. fluminea* is obviously not nearly so well adapted to a "natural" freshwater habitat as are the Pisidiidae.

Ontogenetic events in *C. fluminea* are still very similar to those of marine bivalves, which normally develop *free living* trochophores and veligers. Heterochrony as "phyletic change in the onset or timing of development . . . either accelerated or retarded relative to the . . . rate of development of the same feature in an ancestor's ontogeny," that is in the sense in which De Beer used it (Gould, 1977), — seems evident in the larval development and larval ecology of *C. fluminea.* Since a sexually mature clam can release thousands of well-differentiated, straight-hinged juveniles during a reproductive season (McMahon, 1984) directly into the environment, it would obviously require few such clams to establish a local population quickly. The peculiar development of *C. fluminea* contrasts with that of marine bivalves, which typically rely on planktonic larvae for their distribution. Embryogenesis in *C. fluminea* also contrasts strongly with that of the freshwater Pisidiidae (pill clams and fingernail clams) which produce a very few, large, well-developed young per season. Also, the freshwater Unionidae (Mussels) which individually produce thousands of glochidia larvae that typically

Table 2. Evident heterochrony in the comparative ontogeny of some Corbiculacea: *Corbicula fluminea, Pisidium* and *Sphaerium* Gametogenesis to pediveliger stage.

ONTOGENETIC EVENT*	TIME COURSE OF EVENT	
	Corbicula fluminea	*Pisidium, Musculium*
Oogenesis	precedes spermatogenesis; occurs throughout the year	follows spermatogenesis
Spermatogenesis	follows oogenesis; seasonal, temperature sensitive; "times" reproduction	precedes oogenesis
Sperm	biflagellate	uniflagellate
Cleavage, blastulation	within 24 hours., usually in marsupial gill	——
Gastrulation	usually within 12-24 hrs., in marsupial gill	——
Trochophore	24-48 hrs., in marsupial gill	suppressed
Veliger	24-48 hrs., in marsupial gill	suppressed
Pediveliger	48-96 hrs., in marsupial gill, usually	suppressed
Early juvenile (straight hinge)	24-48 hrs.	? (within marsupial gill)
Late juvenile (straight hinge)	2+ months	? (within marsupial gill)
Shedding* (release from gill)	often as late pediveliger or later	much later in development
Umbonal juvenile	occurs long after shedding when juvenile has attained length of 500+ μm	occurs within marsupial gill
Byssus formation	occurs still longer after shedding when umbonal juvenile attains a length of 1+ μm	*precedes* 1st juvenile stage. occurs within marsupial gill, before shedding, as "placental" byssus.
Gametogenesis	occurs after shedding, after byssus formation, etc.	may occur in "juveniles" within marsupial gill.

*Time course of development, from fertilization (zygote formation) to shedding of late pediveliger or straight-hinged juveniles from marsupial gills of *C. fluminea* is approximately 6-12 days, normally. While in some instances embryos may be retained into late, straight-hinged juvenile stage within marsupial gills, some embryos may be released as early as 5 days after fertilization when the embryos are still pediveligers. Rarely, fertilized eggs, trochophores, or veligers are shed. Trochophores and veligers may exhibit osmotic stress.

require a parasitic period on a specific host fish, contrast with the rapid direct development of juveniles in *C. fluminea.* The ontogeny of *C. fluminea* seems admirably well suited to survival and propagation in the stressed, unstable habitat of many rivers in the U.S. today (Kraemer, 1979; McMahon, 1984). In many ways intermediate between the ontogeny of marine bivalves and of the freshwater Pisidiidae, and neither marine-like nor freshwater-like, the embryology of *C. fluminea* seems well matched to the calamitous events which attend freshwater "ecological crunch" (Wiens, 1977). The heterochronic, ontogenetic "timing" of *C. fluminea* seems very likely to be the main key to its present "success" in U.S. rivers.

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SPAWNING AND EARLY DEVELOPMENT OF *CORBICULA FLUMINEA* (BIVALVIA: CORBICULIDAE) IN LABORATORY CULTURE

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ABSTRACT

The Asiatic clam, *Corbicula fluminea* (Müller), was maintained on the estuarine diatom *Skeletonema costatum* (Greville) in a recirculating aquarium system at 24 to 25°C. Salinity varied from 0 to 8 ppt. Live weight of *C. fluminea* increased from 3% to 179% of initial weight during four months of laboratory culture. The animals then spawned; sperm were ejected out of the exhalent siphons and fertilized eggs were retained in the gills. The first three zygotic divisions occurred 1, 3, and 5 hours after spawning (sperm release), and trochophore larvae developed after 14 hours. Pediveligers were released from parent clams in 4 to 5 days, and metamorphosed to juveniles about 12 hours later. Studies with fluorescent latex microspheres indicated that released larvae were ingesting suspended particles, but brooded larvae were not. Parental broodstock continued to grow under laboratory conditions, and six months after the spawning event, gonad smears of brood-stock revealed gametogenesis taking place.

The exotic bivalve *Corbicula fluminea* (Müller) was first identified in the United States in 1938 (Burch, 1944) and is now widely distributed throughout the country (McMahon, 1982; Counts, 1983). *C. fluminea* has become a pest organism because of biofouling in water treatment facilities, irrigation systems, and power generating stations. Aspects of the reproduction of *Corbicula* spp. have been described (Fuziwara, 1975, 1977, 1978; Kraemer, 1977, 1978, 1980; Kraemer and Lott, 1977; Lee and Chung, 1980; Morton, 1982; Maru, 1981), but difficulties in conditioning and spawning *Corbicula* spp. in the laboratory have hindered detailed examinations of embryogenesis. Sinclair and Isom (1963) were able to maintain *Corbicula* from Tennessee in the laboratory but did not describe growth or spawning of laboratory-cultured animals. Fuziwara (1978) observed ovulation of *Corbicula leana* in outdoor culture ponds, but did not overtly condition the animals prior to spawning, or describe early developmental stages.

General descriptions of larval development of *Corbicula* spp. have been reported (Villadolid and del Rosario, 1930; Cahn, 1951; Sinclair and Isom, 1961, 1963; Britton and Morton 1982), however, most of the illustrations are generalized, and many reports inadequately depict different larval stages. Villadolid and del Rosario (1930) illustrated the larval development of *Corbicula manilensis* from the Philippine Islands, but did not discuss the trochophore larvae. Cahn (1951) described the marsupial trochophores and straight-hinged larvae of *Corbicula leana* from freshwater habitats in Japan. Development of Tennessee populations of *Corbicula* illustrated by Sinclair and Isom (1963) included brief descriptions of trochophores, planktotrophic and benthic veligers. Britton and Morton (1982) discussed and illustrated larval forms of *C. fluminea*, including the marsupial trochophore and veliger larvae.

This paper describes the laboratory culture, spawning, larval development, and larval feeding activity of *C. fluminea*, and compares the results with those of other observers.

TAXONOMY

Bivalves in the genus *Corbicula* von Mühlfeld in the United States have been referred to the taxa *Corbicula fluminea* Müller, *Corbicula leana* Prime, and *Corbicula manilensis* Philippi. Hillis and Patton (1982) presented electrophoretic evidence that two species of *Corbicula* may be present in the United States, but the species question is still under dispute (see, for example Britton and Morton, 1979). Hillis and Patton (1982) recognized two morphological types based on internal shell color (white or purple; the white color form designated *C. fluminea*) and external annulation frequen-

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cy. Our specimens were similar to the white morphotype of Hillis and Patton (1982), and we refer them to the taxon *C. fluminea.*

METHODS

ALGAL CULTURE

Algae that was cultured for feeding clams included the marine flagellate *Isochrysis* aff. *galbana* (Parke), clone T-ISO, the estuarine diatom *Skeletonema costatum* (Greville) Cleve, and several unidentified freshwater algae. T-ISO was obtained from Dr. K. Haines at the University of Texas laboratory, St. Croix, Virgin Islands. Stock cultures of *S. costatum* were obtained from R. R. Guillard, Woods Hole Oceanographic Institution, and *E. gracilis* was obtained from the American Type Culture Collection, Rockville, Maryland. The unidentified freshwater algae mixture was cultured from soil-extract from Lewes, Delaware. Both freshwater and marine cultures were enriched with a modified formulation of f/2 nutrient medium (Guillard and Ryther, 1962; Bolton, 1982).

T-ISO was grown in the laboratory following procedures for marine algal culture described by Bolton (1982). *E. gracilis* and the unidentified algal mixture were grown in freshwater using similar procedures. *S. costatum* was cultured in the same manner as T-ISO, but salinity was reduced from 30 ppt to 5 ppt in stages during culturing; salinity was initially reduced from 30 ppt to 15 ppt, and after two days, salinity was further decreased to between 5 and 8 ppt. Algal cultures at 5 to 8 ppt salinity were harvested semicontinuously for three to five days, and then discarded.

CONDITIONING AND GROWTH OF ADULT *C. FLUMINEA*

Approximately 300 specimens of *C. fluminea* having initial live weights ranging from 1 to 10 g were collected on 9 July 1983 from a freshwater tributary of the Nanticoke River, Nanticoke Wildlife Refuge, Laurel, Sussex County, Delaware, U.S.A. Total live weight of clams was about 1200 g.

For the first two months of laboratory conditioning, clams were maintained in a 200 to 300 *l* recirculating aquarium system at 21ºC and fed a mixture of algae including 25 to 50 *l*/day each of T-ISO, *E. gracilis,* and the mixed culture of unidentified freshwater algae. Cell concentrations of algal cultures were 2 to 3 x 10^6 cells/ml for T-ISO, and 1 to 3 x 10^6 cells/ml for *E. gracilis* and the freshwater algae. Algal concentration in the recirculating system ranged from 125 to 750 cells/ml. Aquarium water was drained and replaced with freshwater every 2 to 3 days, and salinity varied from 0 to 5 ppt.

Because the live weight of *C. fluminea* did not increase substantially during the first two months of culture, water temperature in the recirculating system was increased to 24 to 25ºC and the diet was changed to 180 *l*/day of *S. costatum* (cell concentration of culture was 0.25 to 1.5 x 10^6 cells/ml). Final salinity of *S. costatum* cultures ranged from 5 to 8 ppt, and salinity of water in the recirculating system varied from 0 to 8 ppt.

Growth of adult clams was monitored by measuring live weight of two groups of clams throughout laboratory culture. Clams were labeled with numbered plastic tape and weighed every 2 to 4 weeks. Group 1 contained 17 clams having initial live weights ranging from 0.81 to 9.14 g. Clams in Group 1 were weighed every week for the first two months of laboratory culture and at monthly intervals thereafter for 205 days. Group 2 contained clams having similar initial live weights (1.60 to 2.78 g). Samples of 22 to 30 clams from Group 2 were weighed monthly from day 67 of laboratory culture to day 298.

The dry meat condition index (after Walne and Millican, (1975) was determined for a sample of 20 clams before laboratory culture and for a sample of 18 clams after one year of laboratory culture. Tissue and shell from each clam were separated and dried for 24 to 48 hours at 60ºC, then weighed. The condition index was then calculated by the formula

$$\frac{\text{dry tissue weight}}{\text{dry shell weight}} \times 1000$$

SPAWNING AND LARVAL DEVELOPMENT

Observations of spawning (sperm release) and development of brooding larvae were conducted four hours after aquarium water at 25ºC and 8 ppt was drained, clams sprayed vigorously with 19ºC fresh water, and the aquarium refilled with 19ºC water at 0 ppt salinity. Larval development, therefore, occurred at water temperatures between 19 and 25ºC. Salinity ranged from 0 to 8 ppt during the brooding period following daily algae feedings.

When release of sperm was first observed, gametes were filtered from aquarium water, then stained with acridine orange and observed using epifluorescence microscopy. Gills from one or two parent clams were removed approximately every 1 to 3 hours, and embryos were gently teased from the gills into Petri dishes containing freshwater. Early cell divisions were microscopically examined using embryos freshly removed from parental gills and embryos that were in Petri dishes for up to three hours. The time sequence of successive larval stages was determined by noting the time to the nearest hour after sperm release that each stage was first observed.

Released pediveliger larvae were collected from the bottom of the recirculating reservoir by sequentially filtering water with 212 μm, 125 μm, and 75 μm metal sieves. Most larvae were retained on 125 and 75 μm sieves. Pediveligers were transferred to a 16 *l* aquarium having a sand substratum, and fed 1 to 2 *l* *S. costatum* daily. Water in the 16 *l* aquarium was replaced with freshwater every two days. Shell lengths of 25 to 50 pediveligers were measured weekly to monitor growth.

FEEDING ACTIVITY OF LARVAE

The feeding activity of brooded and released larvae was studied using "Fluoresbrite" fluorescent latex microspheres (Polysciences). Microspheres 3.6 μm in diameter had a maximum excitation wavelength of 540 nm, and were yellow-green in color when examined using epifluorescence microscopy.

Adult clams that were brooding larvae as well as released pediveliger larvae were exposed to algae and microspheres for 6 hours. Algal concentration in the medium was 5 x 10^4 cells/ml and concentration of microspheres was 2.5 x 10^5 spheres/ml. Brooding larvae were removed from the gills of parent clams after exposure to the microspheres and examined using epifluorescence microscopy to qualitatively assess whether or not microspheres had been ingested and were present in the body. Released pediveligers were also examined for fluorescent particles.

RESULTS

GROWTH AND CONDITIONING OF ADULT *C. FLUMINEA*

All clams monitored for growth increased in live weight during laboratory culture. Increase in live weight for clams from Group 1 (initial live weights 0.81 to 9.14 g) ranged from 3% of initial live weight (Fig. 1, clam 16) to 179% of initial live weight (Fig. 1, clam 1). A paired t-test on the initial and final live weights of clams in Group 1 demonstrated that increase in live weight was significant ($t = 11.280$; $P < 0.001$. Clams in Group 2 increased from 2.09 g, standard deviation (s.d.) 0.45 g (Fig. 2) over 164 days of laboratory culture; an increase of 188%. Increase in live weight was significant at $P < 0.001$ (Two-sample t-test; $t = 15.348$).

The condition index of clams after one year of laboratory culture increased significantly, from 67 (s.d. +/– 10, N = 20) at the beginning of laboratory culture, to 115 (s.d. +/– 11, N = 18), after one year of culture (two-sample t-test; $t = 14.085$; $P < 0.001$). This result indicates that increase in live weight of laboratory-cultured clams was due in part to tissue growth, and not due to shell growth alone.

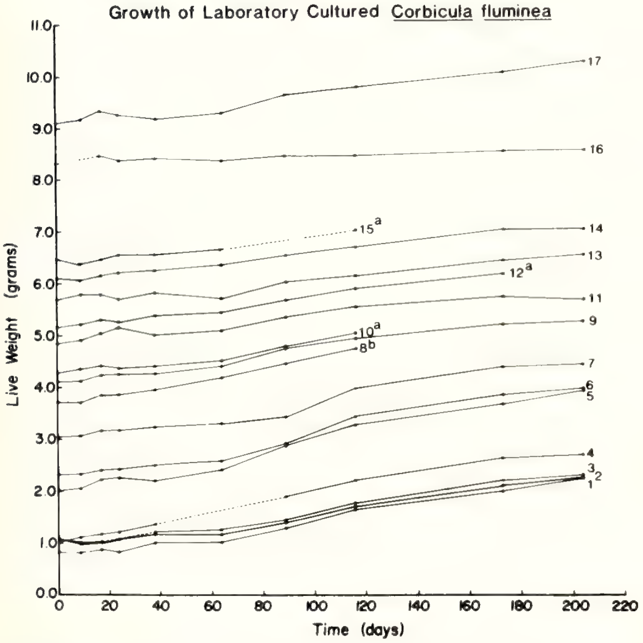


Fig. 1. Live weight of individual *C. fluminea* from Group 1 (initial live weights 0.81 to 9.14 g) during 205 days of laboratory culture. **a.** Label came off clams. **b.** Clam died.

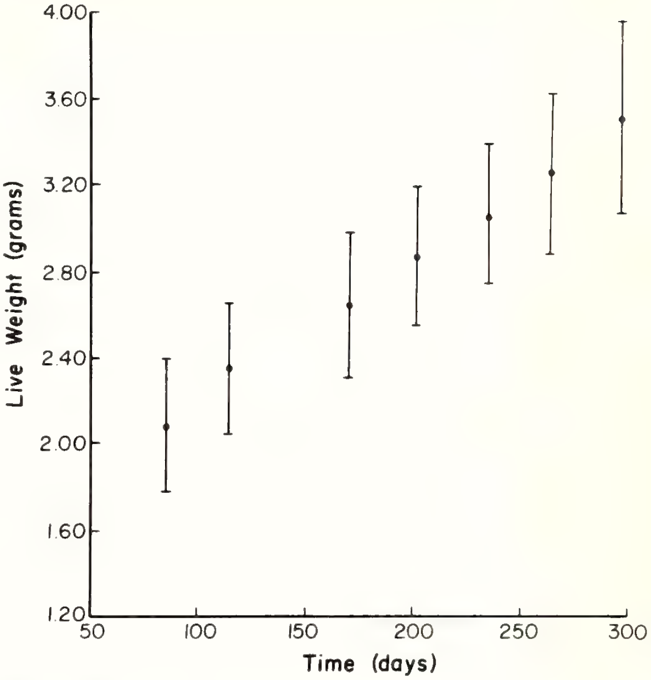
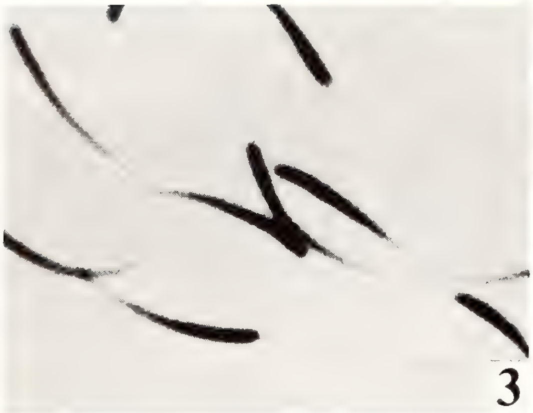


Fig. 2. Mean live weights and standard deviations for 22 to 30 clams from Group 2 (initial live weights 1.60 to 2.78 g) from day 67 to day 298 of laboratory culture.

SPAWNING AND LARVAL DEVELOPMENT

Spawning occurred on 5 November 1983, after four months of laboratory conditioning. Sperm were ejected from the exhalent siphons of adult clams in short bursts. Sperm heads were approximately 16 μm linear distance from end to end (Fig. 3) and bore two flagella. Egg cells, 120 to 170 μm in diameter, were held on the inner demibranchs of the gills of parent clams, and were surrounded by fertilization membranes. Cell counts of gametes filtered from aquarium water during spawning revealed 7.7 x 10^6 sperm cells per ml and only 7 eggs per 500 ml; thus release of eggs by parent clams was negligible, suggesting that fertilization occurred within the clams.

Early cell divisions. The first cell division began about 1 hour after spawning, and the 2-cell stage was complete after 2 hours. The first cell division produced similar sized blastomeres, but in subsequent divisions, cleavage was unequal. The 4-cell to 8-cell stages were first observed 3 and 5 hours after spawning, respectively. Blastulae were first observed 7 hours after spawning, and gastrulation began after approximately 9 hours, at which time the embryo became flattened and developed lobes lateral to the flattened side. Brooding embryos and larvae on the gills of parent clams were encased in a gelatinous envelope that was retained throughout the brooding period (Fig. 4).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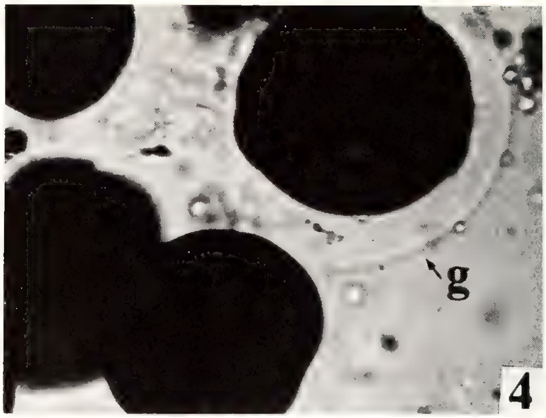

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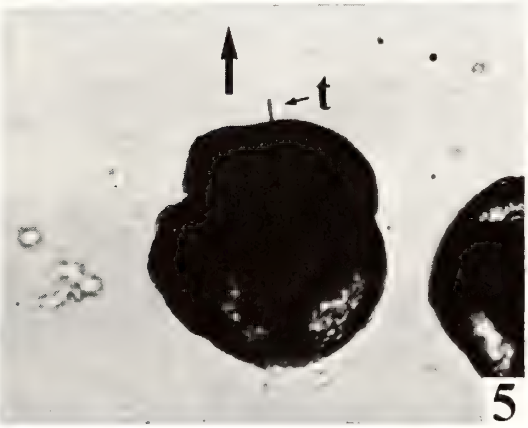

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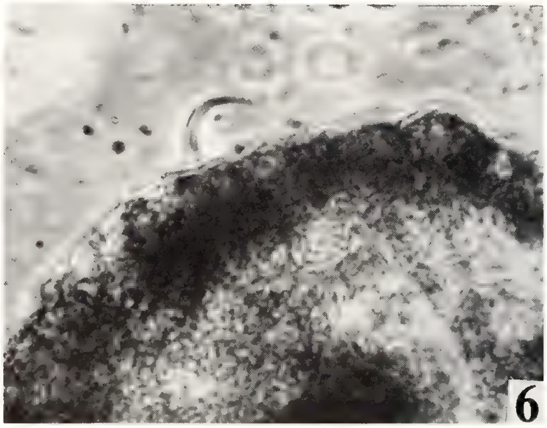
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Fig. 3. Sperm of *C. fluminea* filtered from aquarium water and stained with acridine orange. Horizontal field width = 50 μm. **Fig. 4.** Early embryo of *C. fluminea* surrounded by gelatinous envelope (g). Horizontal field width = 400 μm. **Fig. 5.** Trochophore larva of *C. fluminea* about 20 hours after spawning. Larva was removed from gills of parent clam, liberated from gelatinous envelope and suspended in water. Arrow indicates direction of movement. a = apical tuft. Horizontal field width = 150 μm. **Fig. 6.** Movement of the apical tuft of *C. fluminea* trochophore. Horizontal field width = 55 μm.

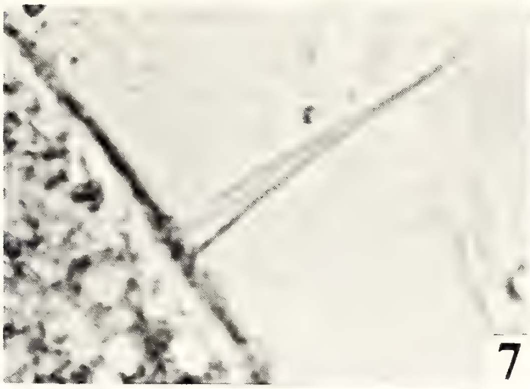
Trochophores. Early trochophore larvae developed after 14 hours (Fig. 5). Cilia were not evident at 14 hours on trochophores that were removed from parental gills, liberated from the gelatinous envelope, and suspended in water, although particles moving in currents around the larvae were observed. Short cilia covering the apical surface were apparent after 17 hours, and at 18 hours much of the surface of the larvae was covered with cilia. Trochophores were immobile while retained on the gills, although larvae that were suspended in water rotated as a result of ciliary activity.

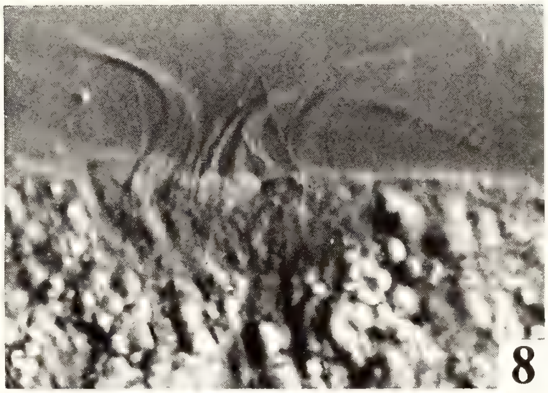
Apical tuft. At 18 hours, trochophores developed an apical ciliary tuft which appeared as a spike-like projection after 20 hours (Fig. 5). When suspended in water, larvae swam with the tuft pointing in the direction of movement. Trochophores removed from the gills flexed and curled the tuft (Fig. 6). Although the tuft initially appeared to be a single, spike-like structure (Fig. 7), photomicrographs magnified approximately 320 x showed that the tuft was composed of individual cilia (Fig. 8).

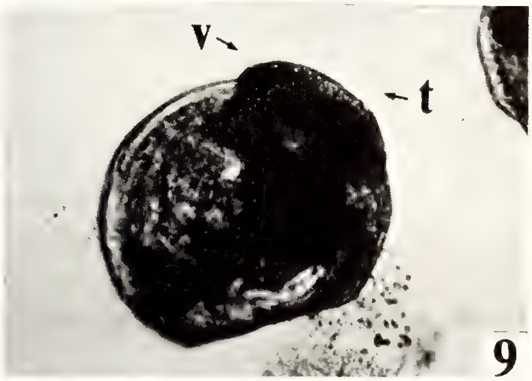
Straight-hinged larvae. Straight hinged larvae (veligers) were first observed at 37 hours and became most prevalent 49 hours after spawning (Fig. 9). The spike-like tuft was retained throughout the straight-hinged larval stage, and extended from the velum. As with the trochophores, larvae that were motionless in the gills became motile when manually freed from the gelatinous material covering the gills, and swam with the velum extended in the direction of movement.

Pediveligers. Pediveligers bearing a spike-like tuft on the velum and a ciliated foot were first released from parental clams at 100 hours after spawning. Some pediveligers remained on the gills of parent clams for 125 hours before release. The gelatinous material surrounding the larvae became less thick and less viscous throughout the period of release.

Juveniles. Released pediveligers shed their vela (metamorphosed) to juveniles at 112 hours (about 5 days) after spawning. Of 21 young clams observed at 112 hours, 67% bore only a foot, 24% bore only a velum, and 9% bore a foot and a velum. All larvae were without vela at six days after spawning. Juveniles were characterized by dark spots on the







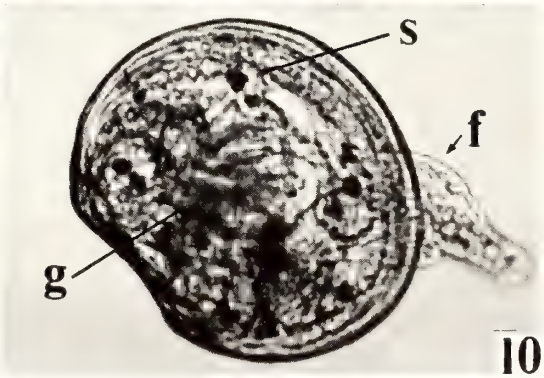


Fig. 7. Apical tuft of *C. fluminea* trochophore. Horizontal field width = 20 μm. **Fig. 8.** Individual cilia of the apical tuft of *C. fluminea* trochophore observed using phase contrast microscopy. Horizontal field width = 40 μm. **Fig. 9.** Straight-hinged (veliger) larva of *C. fluminea* 37 hours after spawning bearing a velum (v) and apical tuft (t). Horizontal field width = 380 μm. **Fig. 10.** Juvenile *C. fluminea* about one month after release from parent. g = gills; s = spot; f = foot. Horizontal field width = 330 μm.

body (Fig. 10), and gills were visible through the shell. The mean shell length of juveniles at metamorphosis was 221 μm (s.d. +/− 10 μm). Shell length increased significantly after one week (two-sample t-test, $t = 10.886$; $P < 0.001$), to 256 μm (s.d. +/− 20 μm). Juveniles became coated with decaying algae and detritus after one to two weeks of culture, and high mortality occurred after three weeks. Remaining juveniles survived for about two months after metamorphosis although little shell growth was observed.

A summary of early development of laboratory-spawned *C. fluminea* is illustrated in Figure 11. The times stated for each developmental stage are based on observations of embryos removed from gills of parent clams, and represent the number of hours after spawning when each stage was first observed, however, as development progressed, gills of parent clams contained brooding embryos at different developmental stages.

Adult clams continued to grow after releasing larvae, and six months after the spawning event, developing eggs and sperm were visible in gonad smears.

FEEDING ACTIVITY OF LARVAE

Particles were visible moving around released larvae as a result of currents produced by the ciliary activity of the velum. Released pediveligers that were exposed to fluorescent latex microspheres contained fluorescent particles within the gut. Larvae brooded on the gills of parent clams showed no gut fluorescence.

DISCUSSION

GROWTH OF ADULT *CORBICULA FLUMINEA*

Culture of *C. fluminea* in the laboratory has been attempted by many investigators using a variety of diets, including strained spinach (Britton and Morton, 1982), and algae, such as *Chlamydomonas, Ankistrodesmus* (Foe and Knight, 1985), *Anabaena, Scenedesmus* (Lauritsen, 1985), and *Chlorella* (Foe and Knight, 1985; Lauritsen, 1985). The diatom *Skeltonema costatum*, fed to clams in the present study, is known to support growth of marine bivalves in intensive culture (Epifanio, 1975). Further investigations of optimal physical and chemical culture conditions as well as nutritional requirements are needed to develop algal diets and culture techniques that support maximum growth of *Corbicula* in the laboratory.

Growth of clams in this study demonstrates that *C. fluminea* is able to tolerate salinities fluctuating from 0 to 8 ppt. Evans *et al.* (1979) reported that *C. fluminea* was able to survive exposures of 10 to 14 ppt salinity without prior acclimitization, and when clams were allowed to adapt to increasing salinity over a period of 40 to 80 days, they observed that *C. fluminea* could tolerate salinities as high as 24 ppt. Although found primarily in freshwater, sparse populations of *C. fluminea* from the Sacramento-San Joaquin estuary, California, USA were found in 17 ppt salinity (Evans *et al.*, 1979). Mouthon (1981) reported populations of *C. fluminea* from France and Portugal in waters of 30 ppt salinity.

SPAWNING AND LARVAL DEVELOPMENT

Spawning (sperm release) of laboratory clams resulted from a combination of thermal, mechanical, and salinity shocks. Induction of spawning under controlled conditions may be possible in future studies by utilizing one or more of the stimuli mentioned above.

Sperm and egg cells of *Corbicula* spp. have been described in different degrees of detail by several investigators. The biflagellate, conical-headed sperm we observed in laboratory spawned clams were similar to descriptions by Britton and Morton (1982) for sperm from *C. fluminea*, and similar to sperm from *Corbicula* from the Ohio River, Ohio, from Newman, California, and from Phoenix, Arizona (Sinclair and Isom, 1963). Sperm from *C. leana* in Japan described by Cahn (1951) are different in size and shape from sperm from American populations of *Corbicula*, and are characterized by a spherical head 2 μm in diameter that bears a single flagellum 15 μm in length.

The reported size of egg cells of *Corbicula* spp. varies. Eggs from laboratory clams ranged from 120 to 170 μm in diameter. Villadolid and del Rosario (1930) reported immature ova 20 to 160 μm in diameter from *C. manilensis.* Ova of *Corbicula* collected from the Cumberland River, Tennessee, were 50 to 120 μm in diameter (Sinclair and Isom, 1963). Britton and Morton (1982) reported egg cells of 280 μm. Variations in the size of egg cells could be due to species differences or environmental conditions, or the developmental stage of the ova at the time of measurement.

The time sequence of developmental stages (Fig. 11) depicts when each developmental stage was first observed, however there was overlap of consecutive stages. Developmental times may vary with water temperature, and were possibly affected by the removal of larvae from parental gills for observation.

Development of early trochophore larvae began with the formation of lobes lateral to the apex, and the later development of the apical tuft (see also Kraemer and Galloway, 1986). Sinclair and Isom (1963) illustrated apical lobes and a ciliary tuft similar to those we observed in laboratory-raised trochophores, and described a later-staged larvae bearing a "flagellum" which was retained during the pediveliger stage. Veliger larvae of *C. leana*, shown by Cahn (1951) bear a tuft resembling a flagellum. Britton and Morton (1982) described an apical ciliary plate on trochophore larvae, but did not discuss a spike-like tuft that we observed in laboratory larvae.

Scanning electron micrographs of trochophore larvae from bivalves in the family Teredinidae have shown that what had previously been described as the apical "flagellum" on the trochophore is in fact a tuft of cilia (Turner and Boyle, 1974; Boyle and Turner, 1976). Our photomicrographs also show that the "flagellum" at the apical region of the trochophore of *C. fluminea* is composed of many cilia which join and move together, and appear as a spike-like projection in later stages.

Although trochophore larvae were motionless when enveloped in the gelatinous layer on the parental gills, the apical tuft of larvae that were manually freed from the gills flexed from side to side, and the larvae swam actively. The tuft possibly has a sensory function that aids in the orientation of the larvae.

Most species in the genus *Corbicula* that inhabit freshwater brood their larvae, and others, primarily brackish water species, release planktonic larvae without an incubation period (Sinclair, 1971; Morton, 1982). The only freshwater bivalve that releases planktonic larvae is the mussel *Dreissena polymorpha,* which inhabited marine environments until the nineteenth century (Morton, 1958; Russell-Hunter, 1964). Marsupial larval development is an advantage for riverine bivalves since planktonic larvae may be carried downstream away from optimal conditions for survival.

The brooding period of larvae from laboratory clams extended 100 to 125 hours (4 to 5 days) after spawning. Eng (1979) estimated a one month incubation period for *Corbicula* populations from the Delta-Mendota Canal, California, USA, however, estimations of brooding periods based on field observations may be influenced by the method and frequency of sampling. In addition, the brooding period is probably affected by environmental conditions (Eng, 1979).

The developmental stage of larvae that are released from parent clams differs among reports. Release of trochophores and earlier developmental stages has been reported (Heinsohn, 1958, cited in Eng, 1979; Kennedy, 1985), which are possibly aborted broods resulting from environmental stress (Heinsohn, 1958). We observed premature shedding of embryos from a sample of clams that were removed from the aquarium and placed in bowls for observation soon after sperm release occurred, however, the majority of larvae were released at the pediveliger stage 4 days later.

Release of nonswimming pediveliger larvae, as observed in this study, or juvenile clams has been reported elsewhere (Cahn, 1951; Sinclair and Isom, 1963; Eng, 1979; Britton and Morton, 1982; Kennedy, 1985). Larvae of *Corbicula* from the Ohio River are reported to spend a short time in the plankton after release, but are not able to use the velum for swimming (Sinclair and Isom, 1963), and become benthic within 48 hours (Sinclair, 1971). Newly-released clams are well adapted for benthic existence; they bear a strong, ciliated foot and are characterized by advanced anatomical organization compared to other bivalve larvae.

Although juvenile clams grew significantly during the first week after release, they appeared to be in poor condition after three weeks, and heavy mortalities occurred. Attachment of juveniles to sand grains using a mucilaginous attachment thread (Kraemer 1979), was not observed in laboratory-cultured juveniles. Further development of culture

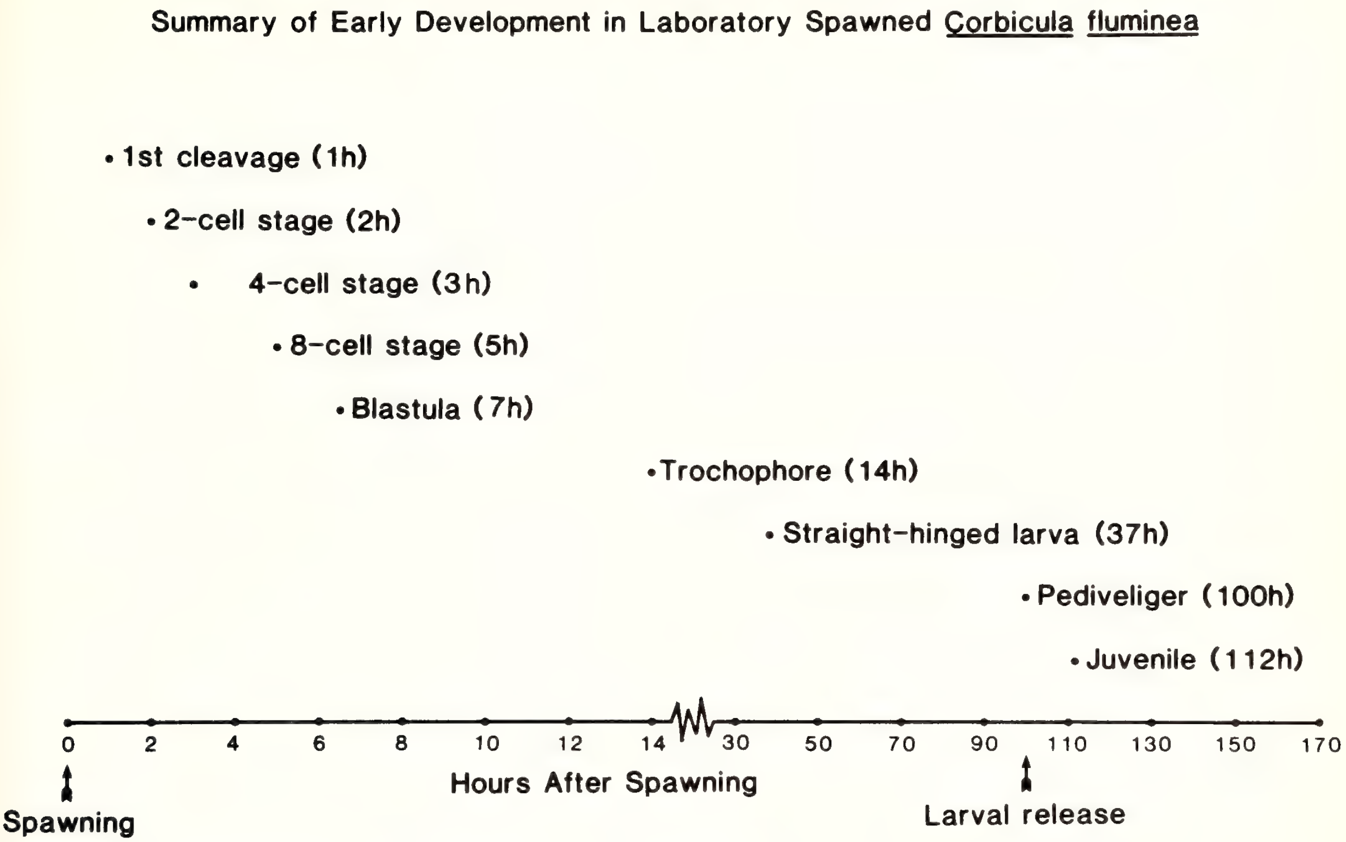


Fig. 11. Summary of early development in laboratory spawned *C. fluminea.*

techniques may enable definition of conditions that induce juvenile attachment.

FEEDING ACTIVITY OF LARVAE

The feeding experiment with fluorescent latex microspheres demonstrated that released pediveliger larvae ingested microspheres, but larvae did not incorporate particles while on the parental gills. More studies on larval feeding activity are necessary to fully understand the nutritive sources for brooding and newly released *Corbicula* (see also Kraemer and Galloway, 1986).

This report is the first account of conditioning and subsequent spawning of *Corbicula fluminea* in laboratory culture. Much more work on laboratory culture of the clams is necessary. Methods to consistently induce release of sperm from conditioned animals will greatly aid in the study of the larval ecology of the clams. Better culture techniques will permit maintenance of clams in the laboratory throughout their entire life cycle and will permit detailed studies on larval development and life history of the organism. Such studies may lead to the development of effective methods for the control of undesirable *Corbicula* infestations.

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EFFECTS OF TEMPERATURE, SALINITY, AND SUBSTRATUM ON LARVAE OF THE SHIPWORMS *TEREDO BARTSCHI* CLAPP AND *T. NAVALIS* LINNAEUS (BIVALVIA: TEREDINIDAE)

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ABSTRACT

Teredo bartschi Clapp was introduced into the effluent of a nuclear generating station at Oyster Creek, New Jersey, in 1974. Normally it maintains breeding populations in Florida and the Caribbean Sea. This species releases pediveliger larvae, capable of swimming and crawling prior to permanent attachment to wood. Field collections of pediveligers were made in the vicinity of Oyster Creek. Laboratory studies compared survivorship and behavioral patterns of pediveligers of *T. bartschi* and veligers and pediveligers of *T. navalis* Linnaeus under various environmental conditions. The purpose of the study was to contrast *T. bartschi* with the native shipworm *T. navalis* Linnaeus, which releases young in the straight-hinge veliger stage.

Pediveligers of *Teredo bartschi* were active between 16-32ºC and 6-35 $^0/_{00}$ salinity, whereas pediveligers of *T. navalis* were active between 10-29ºC and 6-31 $^0/_{00}$. In both species, pediveligers could not tolerate as high a salinity or as low a temperature as adults. At 5 $^0/_{00}$, pediveligers of both species died. As salinity was reduced, pediveligers of *T. bartschi* exhibited a greater tendency to probe wood and burrow. This behavior could be an adaptation in mangrove or estuarine habitats allowing settlement on wood in the mid-range of the salinity gradient.

During the breeding season, pediveligers of *Teredo bartschi* were not often found far from wood and adults, yet the pediveligers do not settle preferentially on wood already containing adults. Clustering of pediveligers causes a highly patchy distribution of adults. Species that release pediveligers have high survivorship and high probability of finding suitable substratum as long as that substratum is abundant and renewable, as it is in tropical mangrove environments.

In 1974, the subtropical shipworm *Teredo bartschi* Clapp was found living and breeding in the heated effluent and marginal areas receiving heated water from the Oyster Creek Nuclear Generating Station, Barnegat Bay, New Jersey (Turner, 1974). It was presumed that this species had been introduced from Florida or another southern locality (Hoagland and Turner, 1980). *Teredo bartschi* has not been found breeding in natural-temperature waters north of Cape Hatteras, but it has been found breeding in the thermal effluent of the Millstone nuclear power plant in Connecticut (Battelle Columbus Laboratories, 1979).

Native species of shipworms in Barnegat Bay are *Bankia gouldi* (Bartsch) and *Teredo navalis* Linnaeus. Larval development of *B. gouldi* occurs entirely in the plankton, whereas *T. navalis* maintains larvae in a brood pouch in the gills until the straight-hinge stage is reached (Culliney, 1975). *Teredo bartschi* also broods its young, but retains them longer until the pediveliger stage is reached (Hoagland, 1983a). Although pediveligers of *T. bartschi* have a well-developed foot and are capable of settling and burrowing almost immediately upon release, they often spend several days alternately crawling and swimming before finally settling and excavating a burrow.

Once *Teredo bartschi* was introduced to Barnegat Bay, it became a potential competitor of native species for the limited wood substratum available. Relative abilities of the larvae and pediveligers to survive and settle under different physical conditions within and outside the thermal effluent at Oyster Creek were of interest. Experiments described in this paper were performed to delimit the abilities of pediveligers of *Teredo bartschi* to survive and metamorphose under a series of temperatures, salinities, and substratum conditions. Whenever possible, data were obtained on straight-hinge veligers and pediveligers of *T. navalis* for comparison.

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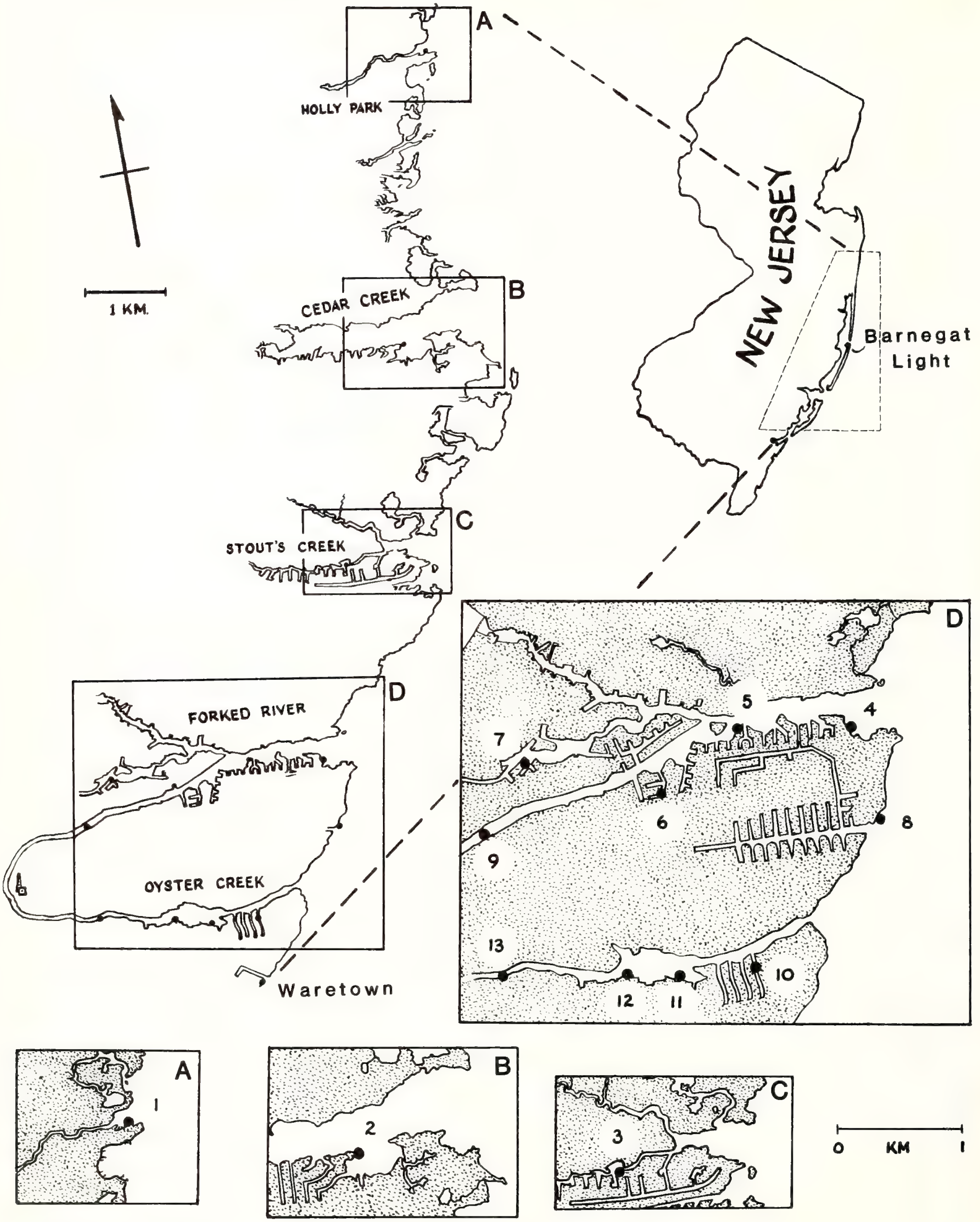
A
HOLLY PARK
1 KM.
CEDAR CREEK
B
NEW JERSEY
Barnegat Light
C
STOUT'S CREEK
D
FORKED RIVER
OYSTER CREEK
Waretown
D
5
4
7
6
8
9
13
12
11
10
A
1
B
2
C
3
0 KM 1

Fig. 1. Map showing the area of study in Barnegat Bay, New Jersey, and its location on the New Jersey coast.

METHODS

White pine panels were used to collect shipworms in Oyster Creek, Forked River, and nearby portions of Barnegat Bay as far south as Barnegat Light between 1976 and 1982 (Fig. 1). Water temperature and salinity were recorded monthly at each collection site. Panels were collected, X-rayed, then dissected to remove shipworms each month. The settlement of larvae was estimated from numbers in panels left in the water 1 month, and the percentage of adults brooding larvae was calculated from dissection of adults taken from panels left in the water 6-12 months.

Live teredinids were obtained from the panels for physiological studies in 1979-1982. Pure cultures of *Teredo navalis* were obtained from Long Beach Island near Barnegat Light (Fig. 1). Panels removed from Oyster Creek in May and in October-November contained pure cultures of *T. bartschi.* The panels were returned to the laboratory once they had become infested with shipworms. After scraping to remove fouling organisms, the panels were placed in holding tanks of 22-24 $^0/_{00}$ salinity and a temperature of about 24 ± 3^{0}C (close to late spring and summer conditions at the collecting sites). Larvae released in aquaria by *Teredo bartschi* and *T. navalis* were collected on Nitex screen sieves and used in salinity and temperature-tolerance experiments. The larvae were fed cultures of *Monochrysis lutheri* and *Isochrysis galbana.* The procedures for culturing shipworms are described in Turner and Johnson (1969), Culliney, Boyle and Turner (1975) and Culliney (1975). Larvae used in experiments were first and second generation, both reared in the laboratory.

A series of temperature and salinity tolerance tests were conducted, lasting from a few hours to several months. Behavioral changes indicated temperature and salinity stress to individual animals. Several types of behavior were categorized for veligers and pediveligers: swimming actively or slowly near the bottom, crawling on a wood sliver or on the culture dish, probing the wood, beginning to bore, pulsating on the culture dish bottom, closed on the bottom, or swollen open and inactive on the bottom. The last two behaviors were indicative of suboptimal conditions if observed with greater frequency than in controls. In each experimental trial, at least 10 juveniles were held per culture dish per experimental trial; most experiments were replicated. The difference in behavior between experimental animals and controls (at fixed temperature and salinity) was recorded.

In all cases, controls were manipulated exactly as were experimental containers, including periods of agitation. Experiments were done in noncirculating filtered seawater changed every 2-3 days, so that close observations could be made and temperature and salinity could be controlled. The health of all species and life history stages would likely be better in an open system, but the comparative aspects of the results here are of value. Also, open systems can introduce unwanted predators.

The following experiments were performed with new animals for each trial; the number of trials per experiment varied and are given with the results. Statistical analyses for comparing results included the chi-square contingency test and Mann-Whitney U-test, as appropriate.

1. SALINITY CHANGE

Pediveligers of both species and straight-hinge veligers of *Teredo navalis* raised at 22 $^0/_{00}$ and 24 ± 3^{0}C were subjected to both rising and falling salinities in separate experiments, 12 pediveligers and 50 veligers per trial, three times in each direction. Salinity was raised gradually from 22 $^0/_{00}$ by adding a concentrated solution of sea salts, a maximum of 3 $^0/_{00}$ per hour. Salinity was lowered at the same rate using dechlorinated fresh water. A pipette-drip system was employed to add water in all experiments, and the containers were aerated to facilitate mixing. The experiment continued until all animals showed stress, with observations made every half hour. The time interval was short because metamorphosis can occur within a few days.

2. RESPONSE TO CONSTANT REDUCED AND RAISED SALINITY

Ten pediveligers per culture dish of *Teredo bartschi* and *T. navalis* were subjected gradually over a 6-hour period at 20-22^{0}C to salinities of 2, 5, 10, 15, 20, 22, 25, 30, 32, 35, 40, and 50 $^0/_{00}$ by dilution or elevation as above. After the target salinities were reached (time zero), observations on behavior were made every 20 minutes for the first 4 hours, then at 6 hours, and then 3 times daily (at salinities 5, 10, 15, 20, 25, 30, and 35 $^0/_{00}$) for 5 days. Two trials were performed.

3. SUDDEN SALINITY CHANGE

Fifteen pediveligers of *Teredo bartschi* per dish at 24^{0}C were subjected to salinity change as above, but more rapidly, either from 22 $^0/_{00}$ to 27 $^0/_{00}$, 22 $^0/_{00}$ to 32 $^0/_{00}$ or 22 $^0/_{00}$ to 12 $^0/_{00}$ over a 2-hour interval. Controls were left at 22 $^0/_{00}$. Observations were made for 15 minutes before and after salinity was changed, and again after it was returned to 22 $^0/_{00}$ over a 2-hour interval.

4. UPPER TEMPERATURE TOLERANCE

While salinity was maintained at 22 ± 1 $^0/_{00}$, temperature was raised 2^{0}C per day, using aquarium heaters. Straight-hinge veligers and pediveligers of the two *Teredo* species were examined, 10 animals per experiment, and behavioral changes were observed over a 5-day period.

5. LOWER TEMPERATURE TOLERANCE

At the constant control salinity, pediveligers of both species were subjected to falling temperatures of 5^{0}C per day and their behavior monitored. Also, *T. bartschi* pediveligers were observed for 5 days at 5^{0}C and at 18-20^{0}C. There were 10-12 animals per test.

6. TEMPERATURE-SALINITY INTERACTION

Pediveligers of *Teredo bartschi* were exposed to 18 identical panels of clear white pine cut from the same board. After the young postlarvae began to bore, they were counted and the panels were isolated from one another in filtered and aerated sea water. Two panels each were established at all

Table 1. Effect of gradual salinity change, *Teredo* species, triplicated. Tabular values are the salinity at which at least 50% of the test individuals were moribund (controls at 22-24 $^0/_{00}$ showed no abnormal behavior). All experiments were performed at temperature = 24 ± 3^{0}C. Sample sizes (N) are in parentheses.

	LOWERED SALINITY $^0/_{00}$				RAISED SALINITY $^0/_{00}$			
Trial:	1	2	3	*Mean*	1	2	3	*Mean*
T. bartschi Pediveligers	7(12)	4(12)	8(10)	6.3	27(12)	35(12)	35(12)	32.3
T. navalis								
Veligers	6(50)	6(50)	—	6	31(50)	27(50)	—	29
Pediveligers	6(12)	6 (12)	—	6	31(12)	—	—	31

combinations of 10, 20, and 30^{0}C and 6, 14, and 22 $^0/_{00}$ salinity.

The water was changed weekly and filtered. The experiment began on 18 February 1981, and was ended on 20 May 1981. Each time the water was changed, it was examined for pediveliger larvae. At the conclusion of the experiment, the panels were X-rayed. The number of specimens per panel and their lengths (mm) were recorded.

7. WOOD PREFERENCE

Behavior of *Teredo bartschi* pediveligers was observed when they were exposed to new wood soaked for 2 weeks in artificial seawater, wood held previously in the field for several months but without shipworms (old wood), and wood from the field containing adult shipworms. Behavioral observations were made after 3 hours, before adults in the wood released additional larvae. Ten individuals were observed on each of four trials. Three behaviors were recognized: swimming, sitting on the bottom of the glass container, or sitting/burrowing on wood.

At the field sites, the distribution of shipworm veligers and pediveligers was observed by taking replicate plankton tows at distances 0-1 m and 2-3 m from the collecting panels. Plankton sampling was done in June, July, October, and November, 1980 and 1981, and in August and September, 1982, in Oyster Creek, Forked River, and Waretown Creek (south of Forked River).

To observe patterns of settlement in the field, white pine stakes 3x7x90 cm were submerged at Forked River, Oyster Creek, and Waretown Creek. Three identical stakes were driven into the mud against the bulkhead at each station, at a slight angle and such that the stakes extended above the water line. The purposes of the experiment were to test the idea that shipworms settle preferentially at the mudline, and to see if the different species have the same settlement preferences. Stations were chosen to maximize the probability of obtaining large sets of all species. One and then two stakes from each station were removed after 4 and 16 months, respectively, and marked as to the orientation of each surface with respect to currents, which were unidirectional in Forked River and Oyster Creek due to operation of the power plant. Mudlines and waterlines were also marked. The stakes were X-rayed and measurements were taken of positions of boreholes, length and direction of growth of burrows. Each individual borer was identified to species.

RESULTS

SALINITY CHANGE

When salinity was raised gradually at 24 ± 3^{0}C, larvae of both *Teredo bartschi* and *T. navalis* withstood salinity higher than found in Barnegat Bay (Table 1). There was no significant difference between species in upper or lower salinity tolerance (Mann-Whitney U-test probabilities >0.2 and $=0.4$, respectively), although pediveligers of *T. bartschi* remained active at slightly higher salinity than did larvae of *T. navalis*. Larvae of both species failed to recover once exposed for over 6 hours to 6 $^0/_{00}$, except for one individual pediveliger of *T. bartschi*, which survived for over a month at 24 $^0/_{00}$ after being kept at 4 $^0/_{00}$ for 10 days. It did not successfully bore into wood.

When salinity was between 15 $^0/_{00}$ and 10 $^0/_{00}$, pediveligers of *Teredo bartschi* increased their crawling and boring activity, relative to swimming. At this salinity range, 50% of test animals exhibited burrowing behavior, as opposed to 20% of controls kept at 22 $^0/_{00}$. All forms of activity fell at 10 $^0/_{00}$; below this level, boring ceased. There was no difference between the responses of straight-hinge veligers and pediveligers of *Teredo navalis*. The behavioral change of both species at 6 $^0/_{00}$ was abrupt. Either abnormal swimming or swelling occurred in all individuals when the salinity was held constant at 6 $^0/_{00}$ for 24 hours.

CONSTANT REDUCED AND RAISED SALINITY

Pediveligers of *Teredo bartschi* maintained at constant changed salinity behaved as summarized in Table 2. Behaviors were pooled into three categories, active, stressed (closed, gaping), or dead, to facilitate comparison of the two species. After 6 hours, behavior indicative of stress occurred at about 5 $^0/_{00}$ and below, and at 32 $^0/_{00}$ and above. Changes in behavior of pediveligers occurred over time, with increased boring activity evident after 2 days at 10-32 $^0/_{00}$. Above 35 $^0/_{00}$, all individuals were closed on the bottom or dead. Below 5 $^0/_{00}$, all individuals gaped or died. Those pediveligers that swam at salinities at and below 10 $^0/_{00}$ did so slowly and in circles near the bottom. Between 15 and 30 $^0/_{00}$, swimming was primarily up and down, and the animals were less frequently near the bottom. After 5 days, a few pediveligers maintained in the range of 10-30 $^0/_{00}$ gaped and appeared stressed, but over twice as many gaping

Table 2. Response of pediveliger larvae to constant salinity (accurate to ± 0.5 ‰) at various levels after 6 hours and 5 days. N = 20 per salinity level. Behaviors are summarized as percent S = stressed (gaping or closed), A = active (boring, crawling, swimming, or pulsating on the bottom), or D = dead.

	T. bartschi						*T. navalis*					
	6 h			5 d			6 h			5 d		
Salinity ‰	A	S	D	A	S	D	A	S	D	A	S	D
2	0	100	0	0	0	100	0	100	0	0	0	100
5	80	20	0	20	80	0	70	30	0	25	75	0
10	100	0	0	65	35	0	50	50	0	75	25	0
15	100	0	0	95	5	0	100	0	0	95	5	0
20	100	0	0	90	10	0	100	0	0	95	5	0
22	100	0	0	—	—	—	100	0	0	—	—	—
25	100	0	0	75	25	0	100	0	0	100	0	0
30	100	0	0	95	5	0	100	0	0	100	0	0
32	80	20	0	—	—	—	90	10	0	—	—	—
35	50	50	0	90	10	0	30	70	0	75	25	0
40	0	100	0	0	0	100	0	100	0	0	0	100
50	0	100	0	0	0	100	0	100	0	0	0	100

pediveligers occurred at 5 ‰ than at any of the higher salinities.

Results for *Teredo navalis* pediveligers were similar to those for *T. bartschi*, except that most pediveligers of *T. navalis* were boring within the 5-day period of the experiment, whereas numerous *T. bartschi* remained motile. This observation is consistent with observations of *T. bartschi* in the holding tanks; larvae of *T. bartschi* survived 14+ days as pediveligers prior to successful settlement.

SUDDEN SALINITY CHANGE

Sudden salinity change from 22 ‰ to 27 ‰ and 22 ‰ to 32 ‰ caused all pediveligers of *Teredo bartschi* to close up and fall to the bottom. Only three individuals of 30 regained activity during 15 minutes of observations. However, when returned to 22 ‰, all larvae began swimming within 15 minutes. Sudden lowering of salinity to 12 ‰ caused less abrupt a response, but within 15 minutes all individuals slowed their swimming or fell to the bottom and pulsated (opened and closed the valves). Likewise, recovery time when returned from 12 ‰ to 22 ‰ was slower; only 12 of 30 individuals resumed active swimming in 15 minutes.

UPPER TEMPERATURE TOLERANCE

Fifty percent inactivity of pediveligers of *Teredo bartschi* occurred as the temperature of the test chambers reached 32° and 33°C in two trials, while 83% of controls maintained at 20°C remained active. Complete inactivity occurred at 34° and 35°C, respectively. Pediveligers of *T. navalis* were 50% inactive at 29°C and 100% inactive at 31°C. The length of time the animals were exposed to each temperature influenced the result; had individuals of *T. bartschi* been left longer at 33 °C, they might have all become inactive at that temperature. Comparatively speaking, however, *T. navalis* showed thermal stress at lower temperature than did *T. bartschi.*

LOWER TEMPERATURE TOLERANCE

Half of the pediveligers of *T. bartschi* were inactive at 16°C. Only three of the 24 individuals showed some crawling response after one day at temperatures of 10°C. In controls maintained at 20°C, 83% of the individuals were active after one day. Pediveligers observed for a 5-day period at 5°C showed no activity past the first day, whereas over half of the control animals kept at 18-20°C were active each time observations were made. When returned to 18-20°C, the pediveligers that had been kept at 5°C all failed to penetrate the wood and died, whereas 55% of the control animals metamorphosed. *Teredo navalis* pediveligers were slightly less sensitive to low temperature. Fifty percent of larvae were still active at 10°C.

TEMPERATURE-SALINITY INTERACTION

Pediveligers of *Teredo bartschi* allowed to bore into wood and maintained for three months at several combinations of temperature and salinity showed the earliest maturation at 20°C and 22 ‰ (Table 3). No release of larvae took place at 10°C, and reproduction was delayed at 6 ‰ salinity (20°, 30°C). Greatest growth occurred at 30°C and the two higher salinities, 14 ‰ and 22 ‰, and at 20°C/22 ‰, although growth was variable among individuals and between replicate panels. The optimal combination for both survival and reproduction was 20°C/22 ‰. Mortality was lowest at the intermediate temperature.

WOOD PREFERENCE: LAB STUDIES

Wood preference experiments in the laboratory showed that *Teredo bartschi* pediveligers settled most frequently on new wood not previously used in Oyster Creek (Table 4). They avoided wood taken from the field, even when it contained adults. Clustering of pediveligers as they settled on the wood occurred whether or not adults were present. A X^2 contingency test on data in Table 4 pooling the trials and comparing new wood, old wood, and wood with larvae versus the three locations of larvae gave a value of 51.5 with 4 d.f., significant at $p < .001$. The cells that deviated most strongly from expected frequencies were the number of pediveligers on wood (significantly large when new wood was offered, but smaller than expected on old wood whether or not adults were present) and the number swimming (large when offered wood containing adults; small when offered new wood).

WOOD PREFERENCE: FIELD STUDIES

Settlement patterns of teredinid larvae on wooden stakes in Barnegat Bay are reported in Table 5. After 4 months, it appeared that most larvae of *Teredo bartschi* settled near the mudline; no such trend occurred for the other species. However, stakes removed after 16 months showed no preferred settlement of larvae near the mudline for any species, and no preferred settlement on the protected sides of the stakes (Oyster Creek and Forked River run in one direction due to pumping of water for the Oyster Creek Nuclear Generating Station). There was a strong tendency for pediveligers of *T. bartschi* to settle in clusters, and for *T. navalis* to be scattered along the length of the stakes. Once metamorphosis occurred, the direction of growth was usually downward with the grain of the wood, although 29 specimens of *Teredo bartschi* were not large enough to measure a direction of growth (Table 5, last line).

Table 3. Survivorship, reproduction, and final lengths of *Teredo bartschi* in various temperature-salinity combinations. Two panels per combination. N = initial numbers per wood panel.

Experimental Conditions		Mean Length (mm)	± S.D.	N	Percentage Mortality	Date of first Reproduction
30°	22 ‰	37.45	15.36	48	15%	Apr. 27
		24.20	10.24	75	8%	Apr. 27
	14 ‰	37.23	10.10	31	42%	Apr. 27
		23.96	8.61	75	25%	Apr. 27
	6 ‰	26.00	9.94	53	15%	May 11
		9.85	4.41	61	69%	—
20°	22 ‰	37.25	15.18	12	8%	Apr. 8
		14.76	5.63	164	0	Apr. 14
	14 ‰	11.09	5.96	44	0	May 11
		14.98	5.64	105	0	May 5
	6 ‰	13.55	7.15	31	0	—
		17.07	8.18	53	0	May 11
10°	22 ‰	4.90	3.06	74	20%	—
		4.24	2.14	17	18%	—
	14 ‰	4.84	2.74	83	53%	—
		2.67	0.58	20	85%	—
	6 ‰	3.22	2.37	50	32%	—
		4.16	3.34	25	40%	—

Table 4. Wood Preferences, *Teredo bartschi* Pediveligers. Sample size is 10 per trial.

	Trial 1	Trial 2	Trial 3	Trial 4	Total
New Wood:					
On Wood	7	6	6	6	25
Swimming	1	0	2	0	3
Lying on glass	2	4	2	4	12
Old Wood with no adults:					
On Wood	0	0	0	2	2
Swimming	4	4	6	5	19
Lying on glass	6	6	4	3	19
Old Wood with adults:					
On Wood	0	0	2	1	3
Swimming	10	6	4	4	24
Lying on glass	0	4	4	5	13

Table 5. Settlement patterns, teredinid species. The data are numbers of individuals.

	Settlement:		Growth:		Borehole Within 10 cm of mudline:	
	exposed	against bulkhead	up	down	yes	no
1980 (4 mo.)						
T. navalis	3	6	2	7	3	6
T. bartschi	5	9	3	11	13	1
1981 (16 mo.)						
T. navalis	4	3	2	5	1	6
T. bartschi	53	26	15	35	0	79

SEASONAL SETTLEMENT

The limited number of plankton samples taken contained no shipworm larvae in June and November, 1980-81. Pediveligers of *Teredo bartschi* were found only within 1 m of bulkheads. They were always common when found, but were found only on two occasions (October, 1980 and July, 1981), and at two of seven stations sampled. Veligers and pediveligers of *T. navalis* were sampled on six occasions, were at more stations (6 of 7), and were found in the samples taken farthest from the bulkheads (2-3 m).

Figure 2 shows the months in which each species taken from panels each month at Oyster Creek and Forked River contained mature larvae in the brood pouch. Figure 3 shows the months in which successful settlement on new panels occurred. These data can be compared against monthly temperature and salinity records for Oyster Creek, Forked River, and control stations (Figs. 4 and 5). Bay controls are stations on the bay, north and south of the thermal effluent area of Oyster Creek, which extends north from Oyster Creek to Forked River and south to Waretown (Fig. 1). Creek controls are stations 3 and 7 inside tidal creeks, representing salinity variation in tidal creeks without the influence of the power plant pumping activity. In every month, adult *T. bartschi* were brooding larvae, whereas none were found in *T. navalis* during January-March. The brooded larvae of *T. bartschi* failed to settle successfully during winter, but settlement was prolonged compared to the native species.

DISCUSSION

SALINITY

It is well-known that salinity affects growth, respiration, and filtration activity of bivalves (Böhle, 1972; Shoemaker, 1973; Van Winkle, 1968). Results reported here are close to those of Blum (1922), who found for adults of *Teredo navalis* a minimum salinity for survival of 6-8 $^0/_{00}$. Hoagland (1983b) found that adults of both species could remain active between 7-45 $^0/_{00}$ at 24°C. These experiments confirm the assertion that bivalve larvae are less tolerant than adults of extremes in salinity. The upper salinity tolerances of these teredinid juvenile stages are far less than those of adults, although lower tolerances are similar.

The difference between adults and larvae of *Teredo bartschi* in lower salinity tolerance was not as great as might be expected, based on the ability of the adult to close off its burrow with its pallets. The upper salinity tolerance was not limiting to adults or pediveligers in the study area of Barnegat Bay, but might be in intertidal tropical mangroves. It may appear that salinity is not a factor limiting distribution of *T. bartschi.* However, under natural conditions, the *T. bartschi* larvae live closer to their lower salinity limits (6-7 $^0/_{00}$) than to their upper limits (35 $^0/_{00}$). Specimens of *T. bartschi* do not grow well and show decreased activity below 10 $^0/_{00}$; this fact is compatible with their distribution in Oyster Creek and lower reaches of Forked River. *Teredo bartschi* have been found in waters that reach salinities of 7.5-30 $^0/_{00}$, but rarely go below 12 $^0/_{00}$ (Fig. 4). The data suggest that healthy, stable populations of *Teredo bartschi* will not exist if salinity remains below 7 $^0/_{00}$ for a considerable time.

Teredo bartschi's ability to tolerate low salinities temporarily is also clear from experiments on sudden salinity change. As in any wild population, there is considerable variation in salinity tolerances among individuals. Wide salinity tolerances of *T. bartschi* enable it to live in estuaries (including mangroves) where sudden but short-term changes in salinity are common due to hurricanes and other natural factors. Rising salinity causes a more instantaneous response in larvae than does falling salinity. It evokes a protective response of closing the shell. Larvae at salinities of 6-7 $^0/_{00}$ or less exhibit gaping, which is probably due to swelling of tissues from failure of osmoregulation. Greater boring activity in *Teredo bartschi* at 10-15 $^0/_{00}$ may increase the probability that the animals will settle at a portion of the estuary optimal for survival.

TEMPERATURE

Failure of pediveligers of *Teredo bartschi* to settle and bore at temperatures below 16°C limits the reproductive period of the species in northern waters, even though larvae can be found in the brood pouches of adults nearly year-round (compare Figs. 2 and 3). Based on temperature alone, one would expect reproduction, larval development and settling in Barnegat Bay, N.J. to occur from sometime after early April to mid-November for *T. navalis* and from about May to late October for *T. bartschi* (Figs. 4, 5). In reality (Fig. 3), *Teredo navalis* settles over a narrower period (late May-early November), and *T. bartschi* occasionally settles as early as April and as late as November. In Florida, *T. bartschi* settles year-round.

The temperature range of *Teredo bartschi* is shifted about 5°C higher than that of *T. navalis*, as expected for a subtropical versus a temperate-zone species. Adults have wider tolerance limits than juveniles because they can survive much lower temperatures than larvae; in experiments parallel to those reported here for juveniles, *T. bartschi* became inactive at 13-17°C while *T. navalis* became inactive at 3-4°C; death occurred at $\sim 3^0$ and 0^0C, respectively (Hoagland, 1983b). Upper temperature limits were similar for larvae and adults.

In Oyster Creek, the upper limit temperature is reached or slightly exceeded in summer, but only for short periods. In winter, even in the thermal effluent, water temperature falls below the minimum for *T. bartschi.* Indeed, heavy mortality did occur every winter for this species, leading me to suspect that strong selection for lower temperature tolerance was occurring. Another possibility was that there was an additional point source of heat entering Oyster Creek, raising the temperature locally. Warm water was found to be entering Oyster Creek from homes near one station, but winter temperature at that point was still only 2-3°C, not appreciably above the temperature of the effluent.

Temperature-salinity experiments showed that minimum temperatures and salinities exist (about 6 $^0/_{00}$ and 10°C) for maturation of *Teredo bartschi* pediveligers regardless of other parameters. Optimal conditions cover a broad range, however. As expected, higher temperature allows more rapid maturation if food is available.

SETTLEMENT

The most surprising result was that involving wood preferences. The common wisdom has been that shipworms settle near the mud line and that they prefer old to newly submerged wood. No aggregation near the water line was detected in the two species examined in this paper, and more settlement occurred on new wood. Attraction to adults did not occur, as it does in some other mollusks.

The limited data on plankton in Barnegat Bay indicate that the presence of pediveligers of *Teredo bartschi* in water is transient and patchy, compared with native species. Although Lane, Tierney, and Hennacy (1954) reported a pediveliger period for this species of only 4 days, it can last four times as long. This is not unusual for long-term brooding species (Turner and Johnson, 1971). The larval stage of teredinids is important as a means of dispersal, not just for feeding, because adults destroy their substratum. *Teredo bartschi* is more patchily distributed than species with planktonic

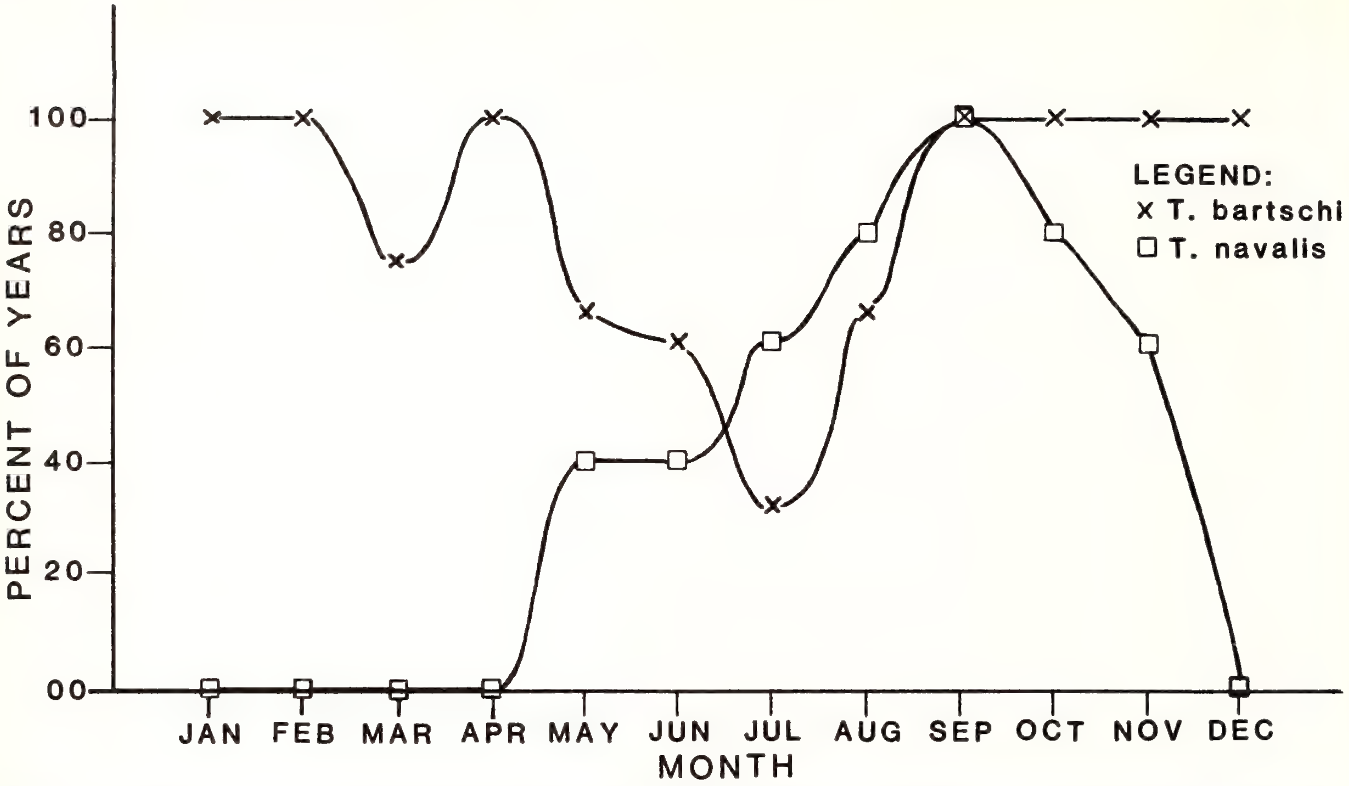

Fig. 2. Percentage of years when mature larvae were present in the brood pouches of *Teredo* species in a given month. The data are for Oyster Creek and Forked River between 1976 and 1982.

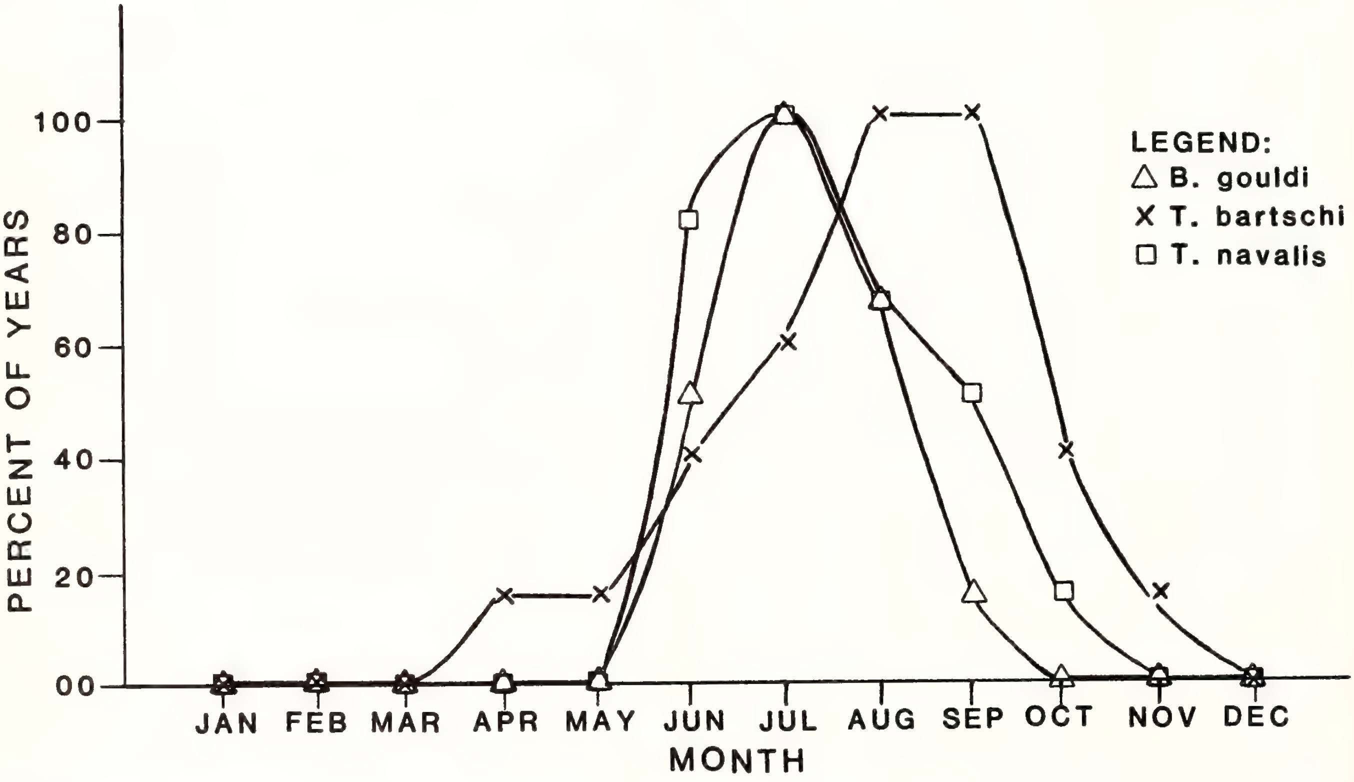

Fig. 3. Proportion of years in which larvae were found settling and boring into wood in a given month. The data are for two *Teredo* species and *Bankia gouldi* in Oyster Creek and Forked River between 1976 and 1982.

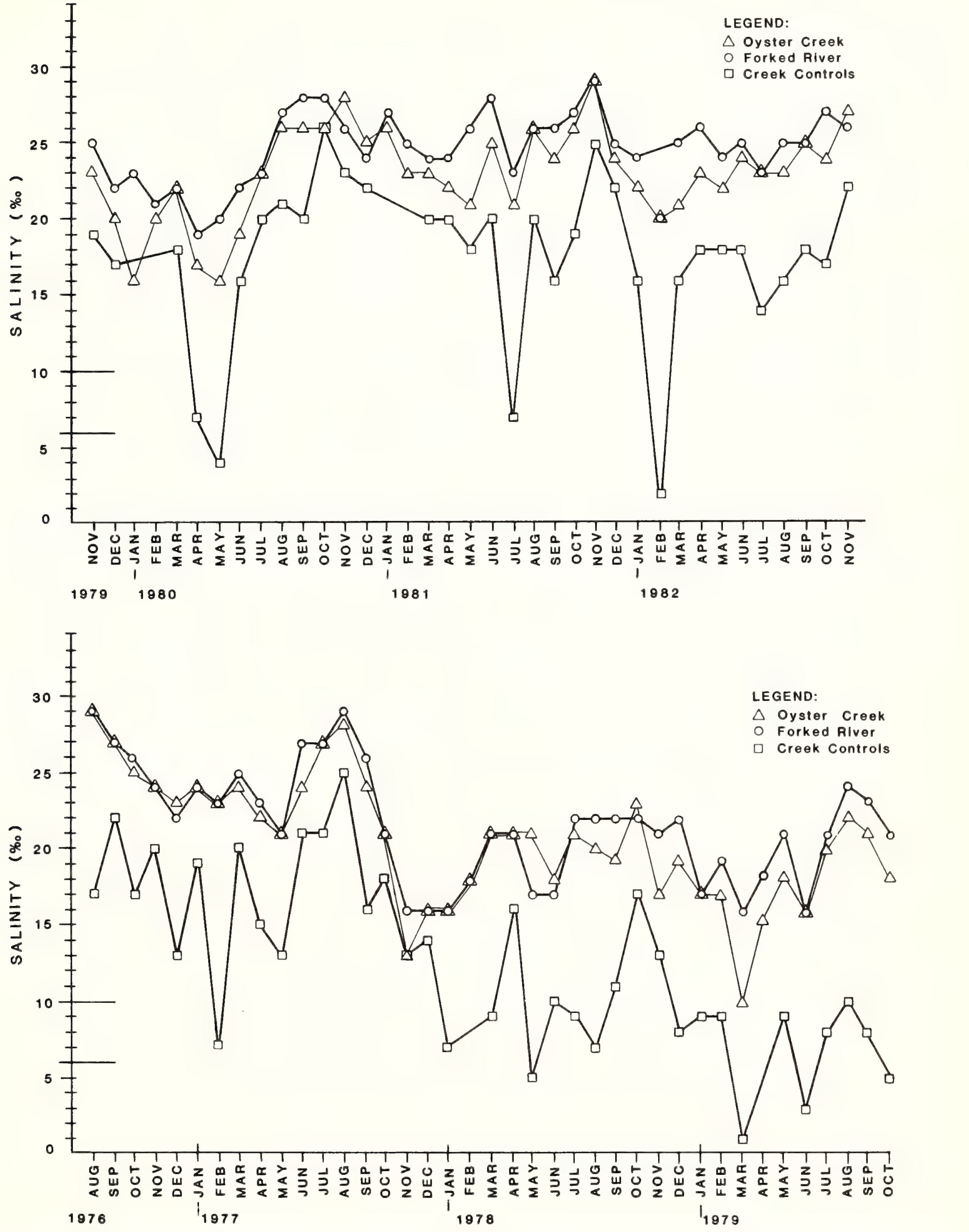

Fig. 4. Averages of monthly salinities in Oyster Creek, Forked River, and control stations, 1976-1982. Bars on y-axis are lower limits for survival (lower bar) and for activity (upper bar) of *Teredo navalis* and *T. bartschi.*

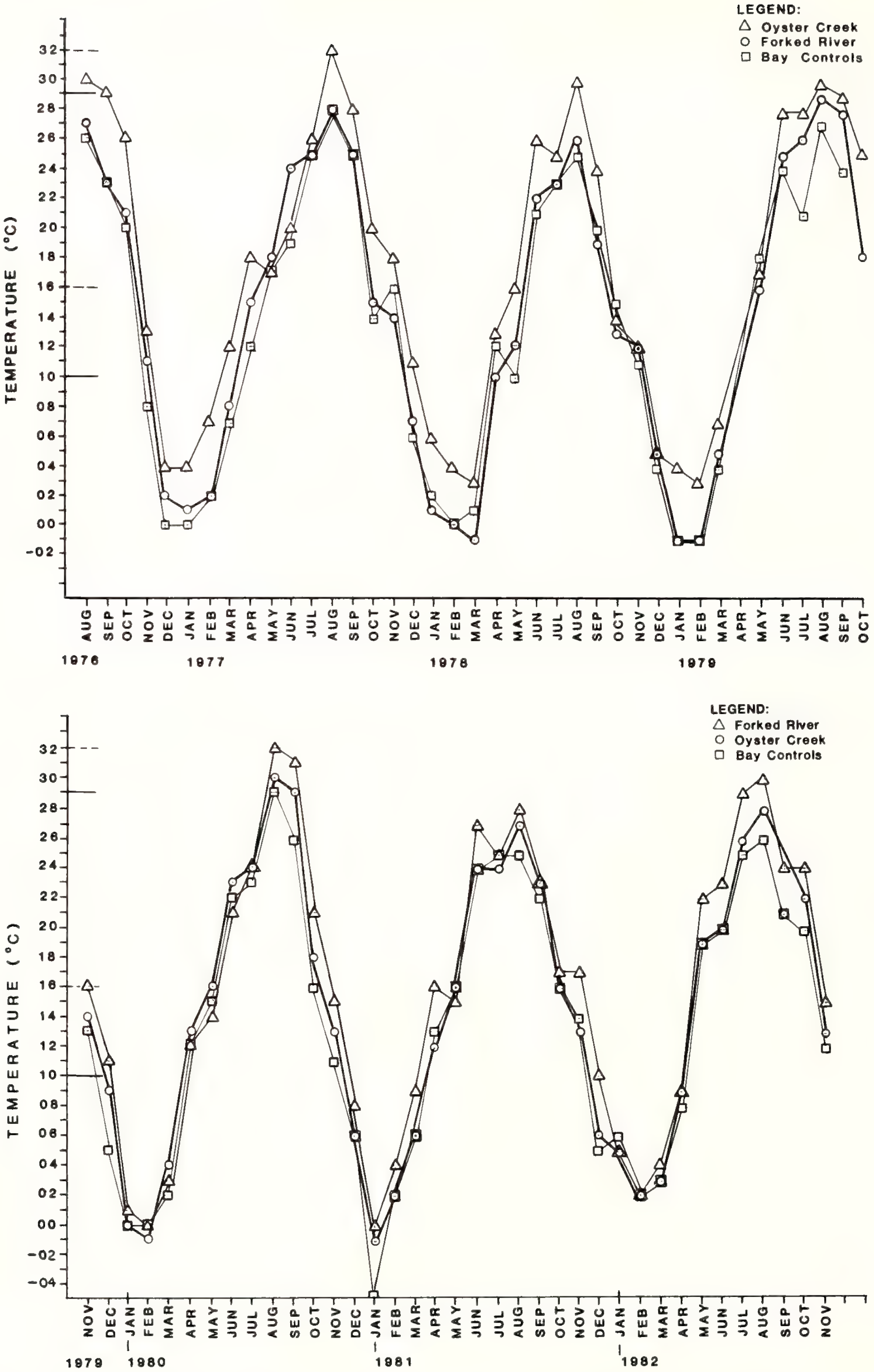

Fig. 5. Averages of monthly temperatures in Oyster Creek and control stations, 1976-1982. Bars on y-axis represent upper and lower limits for reproduction and settlement, *Teredo navalis* (————) and *T. bartschi* (— — — —).

veligers such as *T. navalis*. Most cool-temperature-zone shipworms are released as veligers. Perhaps this is because longer-range dispersal is required where wood is a less concentrated resource than in the mangroves of warmer estuarine waters.

Another conclusion is that the presence of larvae in the gill of *Teredo bartschi* is not indicative of the effective reproductive season in which larvae are successfully released. Nonetheless, the long period over which larvae can be found is another indicator of the flexibility of the species; if temperature and salinity are appropriate, maturation and release of larvae can occur. It is probably this flexibility in timing of larval development, plus the dispersal capabilities of larvae and adults (e.g. in drifting wood) and the likelihood of dispersal of a female with young, which allow *Teredo bartschi* and other teredinids to be such successful introduced species.

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SYMPOSIUM ABSTRACTS

DISTRIBUTION AND RELATIVE ABUNDANCE OF PLANKTONIC CEPHALOPODS IN THE WESTERN NORTH ATLANTIC. Michael Vecchione, Department of Biological and Environmental Sciences, McNeese State University, Lake Charles, Louisiana, USA; **Clyde F.E. Roper,** Department of Invertebrate Zoology, Smithsonian Institution, Washington, DC, USA; **C.C. Lu,** Department of Invertebrate Zoology, National Museum of Victoria, Melbourne, Victoria, Australia; and **Michael J. Sweeney,** Department of Invertebrate Zoology, Smithsonian Institution, Washington, DC, USA.

Cephalopods collected in plankton samples on 21 cruises were identified and enumerated. The 3731 specimens were assigned to 44 taxa. The most abundant and most frequently collected species were the commercially valuable neritic squids *Loligo pealei* and *Illex illecebrosus*. Other abundant taxa included ommastrephids (two species), enoploteuthids (at least five species), onychoteuthids (two species), and unidentified octopods.

Most taxa were distributed widely in both time and in space although some seasonal and mesoscale spatial patterns were recognizable. Most of the neritic species and, surprisingly, the young of the bathypelagic cranchiids appeared to have distinct seasonal distributions. In eight seasonal cruises on the continental shelf of the Middle Atlantic Bight, neritic taxa were collected with approximately the same seasonal patterns during two consecutive years. However, interannual differences in the oceanic taxa collected on the shelf were extreme. The highest abundance and diversity of oceanic specimens were consistently found in the vicinity of the Gulf Stream. Whereas 12 taxa were found throughout the western North Atlantic, five taxa appeared to be limited to either southern or southern and middle latitudes, and three taxa were limited to northern and middle latitudes. Many taxa, though, were not sampled adequately to describe seasonal or spatial patterns.

Comparisons with published accounts of other plankton surveys and midwater-trawl collections indicate both strengths and weaknesses in sampling for the young of oceanic cephalopods. Enoploteuthids were abundant both in this study and in trawling studies from throughout the North Atlantic. Thus, this family probably is adequately sampled throughout its development. In contrast, octopotheuthids and ctenopterygids are rare in trawl collections but comparatively abundant in the present collections as well as in those of other plankton surveys. The commonness of octopoteuthid remains in sperm whale stomachs has been compared with their scarcity in trawl samples to emphasize the difficulty of sampling for oceanic cephalopods. For these families which are relatively common in plankton samples, early-life-history studies, similar to ichthyoplankton surveys, may be the most reliable method of gathering data on distribution and abundance.

RESPONSES TO ENVIRONMENTAL FACTORS BY LARVAL OYSTERS. *(Crassostrea virginica).* V.S. Kennedy and **W. Van Heukelem,** Horn Point Environmental Laboratories, University of Maryland, Cambridge, Maryland.

Responses to a variety of environmental factors (gravity, salinity, light, pressure, haloclines, thermoclines) were measured using oyster larvae from a number of broods hatched in the laboratory. Experiments were designed to address the question of whether or not these larvae were able to respond to environmental cues in a way that would enable them actively to take advantage of estuarine transport upstream. Generally, smaller larvae were negatively geotactic in the dark whereas larger larvae usually became positively geotactic. In the presence of decreased salinity, larvae that had been negatively geotactic became positively geotactic in the dark. As small a decline as 0.4 ‰ from the rearing salinity caused such a switch in geotactic behavior in one brood. Temperature did not affect swimming behavior, whereas swimming speed was directly affected by salinity change. Larvae of all size classes were able to swim through temperature and salinity discontinuity layers of up to 5° and 5 ‰ in extent, respectively. There was no clear indication of larval sensitivity to any particular wavelength or intensity of light. Experiments are continuing in order to gather more data on these matters so our results should still be considered to be preliminary. However, if they remain consistent, our results indicate that oyster larvae are sensitive enough to salinity decrease or increase as to be able to take advantage of estuarine transport mechanisms to avoid being flushed from estuaries under normal conditions.

ECOLOGY OF UNIONOID BIVALVE LARVAE. William H. Heard, Department of Biological Science, Florida State University, Tallahassee, Florida.

Freshwater muteloidean and unionoidean bivalves undergo a form of internal fertilization in the branchial passages or in the interlamellar spaces, and the resulting young are brooded in the demibranchs for various periods prior to their discharge as (in most species) infective larvae that temporarily parasitize the fins or gills of fishes or certain other aquatic vertebrates or metamophosed, nonparasitic juveniles.

Relatively little is known about larval ecology of these mollusks, but some attention has been directed to the following features of larval occurrence and numbers: seasonal gametogenic cycles; marsupial location and volume; superfetation; nutrition of embryos and subsequent larvae during brooding; temporal aspects (neurosecretion, brooding periods, number of broods per year, time of discharge); congeneric variation in larval form; host immunity; and host predation. Marsupial location and volume, brooding periods, and possible hosts have all been shown to vary intraspecifically.

LARVAL DEVELOPMENT AND THE INTRAESTUARINE DISTRIBUTION OF THE HYDROBIID GASTROPOD,

***(SPURWINKIA SALSA)*. Michael Mazurkiewicz,** Department of Biological Sciences, University of Southern Maine, Portland.

Three species of prosobranch gastropods of the family Hydrobiidae occur abundantly in New England estuaries, *Cincinnatia (=Amnicola) winkleyi*, *Spurwinkia salsa*, and *Hydrobia truncata*. Habitats occupied by these minute deposit-feeding snails include shallow subtidal mud bottoms (depth $<$ 3m), intertidal mud flats, tidal marsh turf below mean highwater level and tidal marsh pools at all intertidal levels. From the head to the mouth of an estuary, respectively, populations of these species replace one another, forming a longitudinal sequence of *Cincinnatia-Spurwinkia-Hydrobia* distributional zones. Replacement is gradual, including overlaps in the distribution of *S. salsa* with *C. winkleyi* upstream and with *H. truncata* downstream. Hence *S. salsa* may be found coexisting with either *C. winkleyi* or *H. truncata* but the latter two species never share the same habitat.

The *Cincinnatia* and *Spurwinkia* zones are the least extensive, being restricted to the upper (furthest inland) reaches of estuaries. The Damariscotta River, a central Maine estuary 30 km in length, provides an example. The respective seaward distributional limits of *C. winkleyi* and *S. salsa* lie about 27 and 29 km inland. *H. truncata*, however, ranges from the mouth of the estuary to about 28 km inland.

The restricted intraestuarine distribution of *S. salsa* is difficult to reconcile with the following observations on its larval development and euryhalinity:

1) Indirect development leads to planktotrophic veligers (shell diam. 122-147 μm) that normally remain pelagic 3-4 weeks until settlement and metamorphosis (shell diam. 260-325 μm) during seasonal reproduction from May to October.

2) Females deposit encapsulated eggs that undergo embryogenesis followed by larval emergence at 0-32 $^0/_{00}$, the maximum range of salinities typically recorded in the estuaries. The veligers are remarkably euryhaline, swimming and feeding actively throughout the above salinities. Larval growth and metamorphosis have been observed in laboratory cultures at 5-32 $^0/_{00}$. Serious efforts have not been made thus far to culture veligers below 5 $^0/_{00}$ or above 32 $^0/_{00}$.

3) Benthic juveniles and adults readily survive and remain active at 0-45 $^0/_{00}$. Hypersalinities ($>$ 35 $^0/_{00}$) are occasionally attained in partially evaporated tidal marsh pools inhabited at the highest spring tidal levels. It is presently unknown if reproduction and development can succeed under such hypersaline conditions.

By comparison, *C. winkleyi* and *H. truncata* undertake direct development to benthic juveniles and appear to be less euryhaline than *S. salsa*.The respective ranges of salinity in which *C. winkleyi* and *H.truncata* have been found to survive and maintain activity are 0-25 $^0/_{00}$ and 5-45 $^0/_{00}$.

The marked euryhalinity of *S. salsa* is not surprising since the species is limited to an estuarine sector where the most pronounced salinity fluctuations take place (see Davis, Mazurkiewicz and Mandracchia. 1982. *Proceedings of the Academy of Natural Sciences of Philadelphia* 134: 143-177.) It is also evident that *S. salsa* has the potential for a more widespread colonization of the estuary through larval dispersal. Indeed, qualitative plankton samples have revealed the presence of *S. salsa* veligers in waters of hydrobiid habitats beyond the range of the *Spurwinkia* zone. Future studies on the quantitative spatial distribution of *S. salsa* larvae, their behavior, and settling patterns, will hopefully provide insight on factors governing the distribution of the species. The possibility of interspecific competition influencing the occurrence of *S. salsa* also needs to be examined. That competitive interactions may be important is suggested by apparent habitat displacements of *S. salsa* observed where distributional overlaps occur with either *C. winkleyi* or *H. truncata*. The displacements involve restrictions of *S. salsa* to habitats at progressively lower tidal levels with distance upstream and progressively higher tidal levels with distance downstream. Concurrently, *C. winkleyi* and *H. truncata* replace *S. salsa* in habitats vacated by the latter upstream and downstream, respectively. In both instances, habitats may be found at intervening tidal levels where *S. salsa* coexists with one of the other species. Aside from competitive interactions, physiological-behavioral responses to environmental gradients could also account for these spatial patterns.

BYSSUS-DRIFTING IN LARVAL AND YOUNG POST-METAMORPHIC BIVALVES AND GASTROPODS. John Baldur Sigurdsson, Department of Zoology, National University of Singapore, Singapore.

Byssus drifting is the production in young molluscs of long threads, apparently homologous to byssus threads, for suspension in the water column and subsequent dispersal. Quantitative experimental results show that byssus drifting of young post-metamorphic bivalves and gastropods can be extremely effective, in some cases producing an increase in drag of several hundred times that on an inactive animal, enabling some animals to remain suspended in currents with an upward component as small as 1 mm s^{-1}. With the possible exception of Ostreacea and Teredinidae, byssus-drifting seems to be of universal occurrence in the Bivalvia and includes species that do not have a functional byssus as adults, raising the question whether byssus drifting was the original function of threads produced by the pedal gland, preceding their use for attachment. The ability to prolong the larval pelagic phase by a post-larval byssopelagic phase may be the reason why most bivalves do not seem to conform to the dogma of substratum dependent metamorphosis in marine benthic invertebrates. The literature show that over a hundred species of bivalves have metamorphosed readily and apparently without delay in the laboratoray under most unnatural conditions.

Sampling by means of a fixed near-bottom plankton net has also shown that post-metamorphic planktonic stages of bivalves may be common in the sea, and that some species may have a long post-larval byssopelagic phase. Plantigrades show several special adaptations for byssus-drifting; besides the primary adaptations of a functional filter-feeding mechanism and greatly enlarged larval pedal stem glands for secreting the threads, growth may be arrested or slowed down after metamorphosis and thickening of the shell may be delayed in order to keep the weight of the animal down. Byssus-drifting seems to be widespread in gastropods also and some show the same adaptations as bivalves; arrested growth and delayed thickening of the shell. Some also have an intermediate filter feeding mechanism employed only during the byssus-drifting stage.

SOME ASPECTS OF THE DEVELOPMENT AND BEHAVIOUR OF GASTROPOD VELIGERS OF THE NORTHWESTERN RED SEA. Gamil N. Soliman, Department of Zoology, Faculty of Science, University of Cairo, Egypt.

Studies on the spawning and development of gastropod molluscs of the northwestern Red Sea throughout the last two decades have dealt with more than 40 species of prosobranchs (including a number of coral-boring coralliophilids) and opisthobranchs (mostly dorids but including a few tectibranchs). Prosobranch eggs, laid in cases or capsules, are usually few in number, of large size and lead to the formation of veligers which are not adapted for a long planktonic existence and which shortly metamorphose. Opisthobranch spawns are mostly massive, in the form of tangled strings, coiled ribbons or strings or jelly balls, with large numbers of eggs (up to about 5 million in a single spawn). The majority give rise to planktonic larvae. Of the opisthobranchs studied, only a few species succeeded in metamorphosing under laboratory conditions (some embryos hatched directly in the creeping young stage). Based on studies of behavioral responses to various ecological factors, veligers of intertidal species are exceptionally well adapted for life in such severe habitats.

INTER-RELATIONSHIPS OF LIFE-CYCLE, LIFE-HISTORY AND LARVAL ADAPTATIONS OF NUDIBRANCH MOLLUSCS. Christopher D. Todd and **Jonathan N. Havenhand**, Department of Zoology and Marine Biology, Gatty Marine Laboratory, University of St. Andrews, Fife. Scotland.

The order Nudibranchia in the North Atlantic displays a complete range of larval reproductive adaptations including planktotrophy, pelagic lecithotrophy, non-pelagic lecithotrophy and "direct" development (with vestigial intracapsular larval stages). The majority of species have annual or subannual life-cycles and are semelparous (dying after a period of spawning). A few British species (e.g. *Archidoris pseudoargus* (Rapp), *Jorunna tomentosa* (Cuvier), *Tritonia hombergi* Cuvier)) are biennial yet still semelparous, breeding only at the end of the second year of benthic life. One species of dorid (*Cadlina laevis* (L.)) undergoes an extended iteroparous life-cycle, breeding annually from the end of its second year and surviving for perhaps four to five years. *Cadlina* is further unusual in displaying "direct" development (with crawl-away hatchlings) and producing one, or rarely two, spawn-masses each year. Our broad objective is to attempt a rationalization of the inter-relationships between life-cycle, life-history and larval adaptations within the context of energetic allocations to reproduction. Specifically, we have centered our investigations upon the laboratory analysis of reproduction in the semelparous annual dorids *Onchidoris muricata* (Muller) (planktotrophic larvae) and *Adalaria proxima* (Alder & Hancock) (pelagic lecithotrophic larvae) and the iteroparous *Cadlina laevis. Onchidoris muricata* and *A. proxima* are sympatric, reproduce at the same time of year and preferentially prey upon the bryozoan *Electra pilosa* (L.); *C. laevis* is an exclusive predator of the slime sponge *Halisarca dujardini* Johnston.

Extensive observations of feeding for both A. proxima and *O. muricata* (from post-metamorphic juveniles to adults) showed a broadly similar relationship between body size and feeding rate with asymptotic plateaux at ca. 20 zooids h^{-1} for *A. proxima* and ca. 10 zooids h^{-1} for *O. muricata*. These differences in adult feeding rate are attributable to contrasting radular form and feeding strategy and differences in body size (*A. proxima* adults, 27-63 mg dry wt; *O. muricata* adults, 6-35 mg dry wt.). *Adalaria proxima* rasps *Electra* zooids from the colony while *O. muricata* feeds suctorially. The ability of these two species to continue feeding during the spawning period is of considerable importance to their respective reproductive allocations and indeed it is this particular feature upon which our energetic analyses are focussed.

Seven individuals of *A. proxima* and *O. muricata* were maintained in the laboratory at near-ambient field temperatures from their early post-metamorphic stages throughout their life-cycle. Gross energy budgets (quantifying respiration, growth and reproduction) were constructed for five replicate 7-day periods for pre-reproductive juveniles (September/October 1983) and repeated for the same individuals during the species' respective spawning periods (February/March 1984, *O. muricata;* April/May, *A. proxima*). Although total energy flux (growth plus respiration) for juveniles showed absolute differences (0.50 ± 0.066 J d^{-1} for *O. muricata;* 3.75 ± 0.35 J d^{-1} for *A. proxima*) the proportional allocation of resources to these two components were similar for both species. For spawning adults, however, there are specific differences. For *O. muricata,* spawning adults "degrow" (catabolizing somatic tissues and diverting the products to respiration and/or reproduction) at a rate of $-0.23 \pm .07$ J d^{-1} and allocate 33% of total energy efflux to respiration and 67% to spawn production. Net energy flux for spawning *O. muricata* adults averaged 2.56 ± 0.26 J d^{-1}. For spawning *A. proxima* adults, a contrasting picture emerges with "degrowth" at a rate of -1.90 ± 0.13 J d^{-1}. Net energy flux for spawning *A. proxima* averaged 6.71 ± 0.80 J d^{-1}, of which 48% was accounted by respiration, and 52% by spawn production. As a generalization, therefore, *A. proxima* has somewhat greater respiratory costs and depends upon the catabolism of stored products to a considerable extent in maintaining it reproductive effort. *Onchidoris muricata,* by contrast, maintains a small body size, "de-grows" only slightly, and depends almost totally upon recurrent energy intake from continued feeding to maximize its reproductive effort (i.e. the amount of energy used in reproduction).

Since "de-growth" is an important component of reproductive allocation (especially for *A. proxima*) it is apparent that correlations between total spawn output and simple measures of maximum body size are inappropriate in estimating reproductive effort. Accordingly, we have measured reproductive effort in a dynamic manner by relating the energetic allocation at each spawning to changes in body size between spawnings. This measure is summed throughout the spawning period of each individual to provide a reproductive index (ΣRI), which is given by:

$$\Sigma RI = ((S_t1 - S_t0) - R)/S_t0$$

where S = soma (Joules), R = spawn (Joules) and t = time. If body losses exceed spawn output, a negative index results. In fact, both species display positive indices (data for 21 individuals of both species) but with values for *O. muricata* generally exceeding those for *A. proxima*. It is suggested that the high reproductive effort (perhaps necessitated by the planktotrophic development?) of *O. muricata* demands the ability to maximize recurrent energy flux while maintaining a given body size. The apparent inability of *A. proxima* to perform similarly (and, indeed, its dependence to a large extent on previously accreted somatic resources) is possibly the major factor accounting for selection for pelagic lecithotrophy in this species. Certainly in absolute energetic terms *A. proxima* would, on average, be capable of producing double the number of comparable planktotrophic larvae produced by *O. muricata*.

We have yet to observe and quantify the entire benthic phase for *Cadlina laevis* in our laboratory population. Spawning occurs between November and February and individuals produce only one, or rarely two, spawn-masses. Post-spawning somatic recovery is rapid during the spring months but, curiously, individuals "de-grow" during the late summer/autumn period prior to spawning again. Fecundity and reproductive effort apparently increase with age (but not necessarily size), as theoretically predicted for individuals of decreased residual reproductive value, and is an order of magnitude lower than for *A. proxima* which is itself an order of magnitude lower than for *O. muricata*.

Energetic studies of *Cadlina* are incomplete but preliminary observations of respiration and growth rates show that both are very low for this species. The first spawning occurs at the age of two years. Studies currently in progress continue to attempt resolution of inter-relationships between respiration rate, growth rate, total energy fluxes, life-cycle and life-history as correlates of larval adaptions. We believe that these may well provide informative insights to the bewildering question of why these ecologically similar species have adopted such contrasting larval types: the answer cannot simply lie in historical accident.

THE ABUNDANCE AND VERTICAL DISTRIBUTION OF LARVAL *PLACOPECTEN MAGELLANICUS* AND OTHER BIVALVE LARVAE IN COASTAL NOVA SCOTIA.

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The sea-scallop *(Placopecten magellanicus)* is of major commercial importance to Atlantic Canada and the northeast United States. The population size of the commercial beds (e.g. Bay of Fundy, Georges Bank) fluctuates tremendously. Two studies of catch levels in the Bay of Fundy scallop fishery (Dickie, 1955; Caddy, 1979) have suggested that the fluctuation in year-class size is a function of the degree to which scallop larvae are retained within the Bay. However, to date there have been no systematic studies of larval sea-scallop distribution.

We studied sea-scallop larval distribution in a non-commercial scallop bed in southwest Mahone Bay. The area has a depth range of 5 to 20 m and was well mixed during the sampling period of August to November. Plankton samples of approximately 1.5m^3 were obtained with a high-volume pump system at least once per week at five depths: 1m, 4m, 7m, 10m, and 20m off the bottom. Samples were collected on 64 μm mesh after passing through 333 μm mesh to filter out larger planters.

We were tentatively able to identify scallop larvae using a light microscope and were able to confirm our identifications by examination of the hinge structure using scanning electron microscopy. Scallop larvae ranging in length from 130 μm to 260 μm were found from September 19 until October 19. During this time the water column was isothermal and temperatures declined from 17ºC to 13ºC. Concentrations of scallop larvae were low compared to other bivalves. Averaged over the upper 10 m, scallop larvae generally numbered less than 1 m^{-3} while *Modiolus modiolus* larvae usually numbered between 10 m^{-3} and 100 m^{-3}.

Because few scallop larvae were found on any given sampling date, only a composite picture of vertical distribution over the period September 19 to October 19 could be constructed. Scallop larvae were found at all depths but were taken in greatest numbers at 4 m depth, with lowest numbers observed in the deepest sample.

Other bivalve larvae in the area included *Anomia* sp., *Mytilus edulis*, and *Mulinia* sp. *Modiolus modiolus* larvae were among the most abundant bivalve larvae. Thus, we present *Modiolus modiolus* as a model for bivalve larval distribution in the Bay of Fundy. Sampling over a 12 hour period (3 series of samples on the ebb tide and 3 on the flood) at one station showed a statistically significant change in the depth distribution of *M. modiolus*. During the flood tide, larvae of 150-250 μm length were distributed relatively evenly over the upper 10 m, with a sharp reduction in numbers at 18 m. During the ebb tide however, most larvae were found at the 1 and 4 m depth. Whether the change in depth was actually a reflection of vertical movement by the larvae, or the sampling of a different group of larvae as it passed by the station cannot not be resolved. Because the vertical position of bivalve larvae does change, these changes must be considered in any models of larval transport based on current structure.

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Full manuscripts or abstracts of the Ecology of Freshwater Molluscs Symposia (Organized by Eileen H. Jokinen) and the Encapsulation of Embryos by Molluscs Symposia (Organized by Jan A. Pechenik) will appear in upcoming editions of the *American Malacological Bulletin.*

ABSTRACTS

ORIGINS OF THE MOLLUSCAN FAUNAS OF THE AFRICAN GREAT LAKES: NEW EVIDENCE. Kat, P.W. National Museum Kenya, Nairobi.

Two lines of evidence, one fossil and the other karyological, are persued to elucidate the origin and evolution of the endemic molluscan faunas of the African great lakes. An early Miocene fauna from the Gumba beds on Rusinga Island in Lake Victoria shares several taxa with that of the contemporaneous Mohari Formation of the Edward-Albert Rift, indicating the existence of a widespread pre-rift fauna. During the Miocene, there was an apparent radiation of the bivalve genus *Pliodon*, which is first encountered in the Cretaceous, and is now represented by two species with relictual distributions: *P. ovata* in West Africa and *P. spekii* in Lake Tanganyika. Neither Miocene fauna contains representatives of the presently widespread gastropod genus *Bellamya* and the bivalve genus *Caelatura*, which are proposed to have invaded Africa from Central Asia when a land bridge formed about 17 mya.

Karyological evidence indicates that all species of *Bellamya* in Lake Victoria are derived from Nilotic *B. unicolor*; their chromosomal identity indicates a recent radiation. A new species of *Bellamya* from the coastal region of East Africa, previously included in *B. unicolor* on the basis of shell shape similarities, is entirely different in chromosome number and morphology. At least two races of this new species exist. Further south, widespread *B. capillata* and the endemic *B. jeffreysi* from Lake Malawi, while different in chromosome number, hybridize freely. The resulting hybrid swarm of sterile individuals is mainly found in shallow water in the southern region of the lake. *B. capillata* and *B. jeffreysi* exhibit a distant relationship to the coastal region species. *Neothauma tanganyicense* from northern Lake Tanganyika shows an expectedly high chromosomal similarity to *Bellamya* from both Lake Malawi and Lake Victoria. These observations necessitate a complete revision of the African Viviparidae, the present taxonomy of which relies too heavily on shell parameters.

NEW RECORDS FOR SEVEN APLACOPHORUS MOLLUSCS FROM THE EASTERN GULF OF MEXICO, WEST COAST OF FLORIDA. James K. Culter and **Nora V. Maddox,** Mote Marine Laboratory, Sarasota, Florida.

The distribution, abundance and taxonomic status of the aplacophorus molluscs is poorly known. This group is probably not as rare as would be suggested by accounts in the literature. Due to their small size, they are perhaps often overlooked in ecological studies.

From November of 1979 through July of 1984, aplacophoran specimens were collected from three regions of the west Florida Coast, in waters ranging from 1.5 (nearshore) to 150 meters deep (approximately 150 miles offshore). The majority of specimens were found at depths between 80 to 150 meters. The study areas were bounded by the Dry Tortugas to the south and the Withlacoochee River to the north. Ninety-six stations were sampled over all seasons with aplacophorans present at 25 (26% of total). A total of 2,656 samples resulted in the collection of 473 aplacophoran specimens. Two quantitative sampling devices were used for the collections: a modified Reineck box core (sampling area $0.045m^2$) and a diver-operated box core (sampling area $0.0156m^2$). A 0.5mm mesh size was used to separate infauna from sediments.

A total of 7 undescribed species, as distinguished by external characteristics, were differentiated. Six of the species belong to the subclass Solenogastres and the remaining species to the subclass Caudofoveata. Four species (1 caudofoveata, 3 solenogastres) accounted for over 98% of the animals collected. Specimens were recoverd from sediments ranging from silt/clay to coarse sand with majority of specimens present in fine (57% of total animals) to medium sand (36% of total animals). These collections represent a new record for the eastern Gulf of Mexico.

POLYPLACOPHORA AND FISSURELLIDAE (MOLLUSCA) IN THE NEWPORT RIVER — BOGUE SOUND REGION OF NORTH CAROLINA. Hugh J. Porter. University of North Carolina at Chapel Hill, Institute of Marine Sciences, Morehead City.

A 1981-1985 survey of chiton and limpet populations in the Bogue Sound — Newport River — Beaufort Inlet, NC channel areas found *Chaetopleura apiculata* (Say, l834), and *Diodora cayenensis* (Lamarck, 1822) in the eastern and western inlet regions of Bogue Sound, southern mouth of Newport River, and Beaufort Inlet. Distributions seemed limited by salinity, food, and available shell substrata. Fauna within shell substrata of high chiton densities were discussed. Evidence of xanthid predators as a density limiting factor within shell substrata was discussed.

Highest densities of *C. apiculata* were from just west of the Morehead City State Port in Bogue Sound and west of Phillips Island in the mouth of the Newport River — 55/bu and 30/bu respectively of dredged shell. These same areas also had the highest densities of *D. cayenensis* (3.5/bu and 2.2/bu respectively.

Length data from the State Port and Phillips Island *C. apiculata* populations were suggestive that the species has a 2+ year life span in North Carolina waters. Possible reasons for *Chaetopleura* from the Phillips Island bed to be significantly larger in length than those from the State Port bed were examined.

A second chiton species, found at Wreck Point in the bight of Cape Lookout (just SE of Beaufort Inlet) in 1981, was identified as *Ischnochiton striolatus* (Gray, 1828) (W.G. Lyons, Florida Dept. Nat. Resources).

This species was found in all samples from the State Port bed (highest density = 11/bu dredged shell), only twice from the Phillips Island bed, Cape Lookout, and at no other locations. Specimens were considerably smaller than those recorded from areas further south; length means from the State Port bed ranged between 4.9 and 6.3 mm. This occurrence is an extension of the northern range of *I. striolatus* from Florida to North Carolina.

THE *STROMBUS COSTATUS* COMPLEX IN THE NEOGENE OF SOUTH FLORIDA. David Hargreave, College of General Studies, Western Michigan University, Kalamazoo.

Collections of material from the Pliocene and Pleistocene fossil beds of South Florida have uncovered four distinct members of the *Strombus* subgenus *Tricornis*, all apparently related to one another and to the extant species *Strombus costatus* (Gmelin). The oldest member is an as yet unnamed form from the Pinecrest Beds exposed in the vicinity of Sarasota. A second unnamed form, also tentatively assigned to the Pinecrest Beds, is presently known only from the Mule Pen Quarry northeast of Naples. The third form, *Strombus leidyi* (Heilprin), is limited to the Caloosahatcheee marls and was the first fossil member of the subgenus known from the New World. The youngest member of the group is *Strombus mayacensis* (Tucker & Wilson), which is limited to the early Pleistocene Bermont Beds. Traditionally, *Strombus leidyi* has been thought to be the immediate ancestor of *Strombus costatus*, with some seeing the former as merely a tall-spired form of the latter. A study of shell morphology within the group demonstrates that these two species exhibit significant differences in overall shell size, body shape and many aspects of shell sculpture, but interestingly no statistically significant difference in their relative spire heights. *Strombus leidyi* can be easily separated from all other members of the group on the basis of spire shape and various features associated with the area of posterior lip attachment. Likewise, the unnamed form from the Pinecrest Beds at Sarasota can be separated from all other members of the group on the basis of elements of sculpture of the body whorl together with the absence of lirations on the parietal wall below the point of lip attachment. In all other respects, it is the member of the group morphologically most similar to *Strombus costatus*. Further study of the group is indicated to determine the phylogenetic relationships among its members as well as their relationships to both fossil *Strombus* from the Gatunian Province and extant species in the Panamic Province.

RAPID MORPHOLOGICAL EVOLUTION IN A NEW ENGLAND PERIWINKLE SNAIL. Robin Hadlock Seeley, Department of Biology, Yale University, New Haven, Connecticut.

Proponents of the punctuated equilibrium theory in evolutionary biology maintain that natural selection has relatively little to do with episodes of rapid and significant morphological change in the fossil record, and that morphological evolution is concentrated in speciation events. Testing these hypotheses is difficult because episodes of rapid morphological change are rarely seen in living species, where the processes of natural selection can be observed and where morphological differences between taxa can be compared to genetic differences between those taxa. One such episode, however, has occurred recently in an intertidal snail in Maine (USA). The shell morphology of *Littorina obtusata* (L.) has changed markedly during the last 100 years. Snails in the late 1800's had tall spires and thin shell walls. In contrast, snails in the late 1900's (in southern and mid-coastal Maine) have flat spires and thick shell walls.

This change in shell morphology evidently traces to increased predation by green crabs *(Carcinus maenas* (L.)), since flatter, thicker shells reduce a snail's vulnerability to crabs. One line of evidence for this is the strong correlation between snail shell morphology and abundance of green crabs in the 1980's: spire height decreases and shell thickness increases with increasing green crab abundance. A second and more direct line of evidence for the effect of crabs on snail shell morphology comes from field experiments. When snails of the two shell forms were tethered in the intertidal zone, flat snails survived longer than tall snails at sites where green crabs are abundant. At other sites where green crabs are rare, survival of flat and tall snails did not differ. Finally, electrophoretic analyses indicated that snails producing these different shell forms are members of one morphologically variable species. These data indicate that natural selection can produce a major morphological change over a short period of evolutionary time, and that significant morphological evolution can occur without speciation.

REVISION OF GENERA AND INDO-PACIFIC SPECIES IN THE FAMILY ARCHITECTONICIDAE. Rüdiger Bieler, Department of Invertebrate Zoology (Mollusks), National Museum of Natural History, Smithsonian Institution, Washington, D.C.

The Architectonicidae is a family of gastropods with a worldwide distribution in subtropical and tropical waters, known to feed on coelenterates. Approximately 50 generic names have been proposed for or used in this family. The Recent and fossil genera have been revised, based on a system of homologous sculptural elements of the teleoconch. Additional characters of size, shape, sculpture and coloration of teleo- and protoconchs, as well as anatomical, radular and opercular data support the proposed system. The Recent species (approximately 130 worldwide) can be grouped in the following generic and subgeneric taxa:

Architectonica (Architectonica) RÖDING, 1798
Architectonica (subgen. nov.) [in press]
Philippia (Philippia) J.E. GRAY, 1847
Philippia (Psilaxis) WOODRING, 1928
Philippia (Basisulcata) MELONE & TAVIANI, 1985
Discotectonica MARWICK, 1931
Granosolarium SACCO, 1892
Solatisonax IREDALE, 1931
Pseudotorinia SACCO, 1892
Pseudomalaxis (Pseudomalaxis) FISCHER, 1885
Pseudomalaxis (Spirolaxis) MONTEROSATO, 1913
Heliacus (Heliacus) ORBIGNY, 1842
Heliacus (Torinista) IREDALE, 1936

Heliacus (Grandeliacus) IREDALE, 1957
Heliacus (Teretropoma) ROCHEBRUNE, 1881
Heliacus (Gyriscus) TIBERI, 1867
Heliacus (subgen. nov.) [in press]

The remaining nominate genera are either only known as fossil forms, or are regarded as not available, as synonyms or as non-architectonicids.

A revision of the Indo-Pacific species of the family has reduced the number of species from more than 160 available names to 85 considered valid. Most of the species have a wide geographic range, some of them showing a continuous distribution from Africa to the American West coast. This can be explained by the long-lived teleplanic larval stages of architectonicids.

THE TROCHID GENUS *LIRULARIA* DALL, 1909: A FILTER FEEDER?

James H. McLean, Los Angeles County Museum of Natural History, Los Angeles, California.

Lirularia is a small-shelled genus (shell height 3-7 mm) with variegated color patterns, associated with rock and algal habitats in shallow water. Seven species are known in the northeastern Pacific and two from the northwestern Pacific. It has long been known that the rhipidoglossate radula of *Lirularia* species is of the umboniine type with reduced shaft and cusps. Fretter (1975) showed that the gill of *Umbonium* is monopectinate, with greatly elongated filaments attached only at the base (unlike the monopectinate ctenidium of higher prosobranchs in which filaments are fused to the mantle skirt) and that the epipodial structures are modified to assist in filter feeding. For this study, a specimen of *Lirularia lirulata* (Carpenter, 1864), the type species of *Lirularia*, was relaxed in $MgCl_2$, removed from the shell, fixed in Bouin's, critical-point dried, and gold-coated for examination with SEM.

The gill of *Lirularia* resembles that of *Umbonium*, although there are fewer filaments. As in *Umbonium* (and other trochids), each filament has a prominent "sensory bursicle", as first described by Szal (1971). The frontal, lateral, and terminal cilia of the filaments are readily apparent when examined with SEM. A ciliated tract on the right side of the mantle cavity evidently functions as a food groove, where it is overlain by the tips of the filaments. The snout of *Lirularia* is broad like that of most trochids (unlike the narrowed snout of *Umbonium*), although the tip of the snout has a ringlet of small tentacles that lack sensory cilia; similar tentacles occur on the snout of *Umbonium*. The left neck lobe of *Lirularia* is digitate (as in many other trochids), not expanded to form a siphon enveloping the left cephalic tentacle, as in *Umbonium*. Unexpectedly, tufts of sensory cilia were found on the neck area, extending within the mantle cavity; similar structures were not found in four other trochaceans that were also examined with SEM.

The homology of the radula, gill filaments, and snout tentacles clearly indicate that *Lirularia* is related to *Umbonium* and should continue to be placed in the trochid subfamily Umboniinae. Field studies are needed to determine the importance of filter feeding in the feeding budget of *Lirularia*, as most other prosobranch filter feeders also have the capacity to ingest food in more conventional ways. *Lirularia* moves rapidly; it is unique among prosobranch filter feeders in being neither infaunal nor epifaunal and sedentary. The evolutionary origin of *Lirularia* is another problem: it could represent a step in the specialization leading to *Umbonium* or the return to a hard substratum of an infaunal umboniine.

CLYPEOMORUS, A GENUS OF LITTORINID-LIKE CERITHIDS.

Richard S. Houbrick, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

The prosobranch genus *Clypeomorus*, dating from the Miocene, is endemic to the Indo-Pacific, and represents a major cerithiid adaptive radiation into intertidal hard substratum habitats. The genus is characterized by low spired, frequently beaded shells and all species are eurytopic, style-bearing herbivores, having taenioglossate radulae. Pallial gonoducts are open, males are aphallate and produce spermatophores. Development planktonic or nonplanktonic. Twelve living species are recognized: *C. bifasciata* (Sowerby), *C. brevis* (Quoy and Gaimard), *C. batillariaeformis* Habe and Kosuge, *C. pellucida* (Hombron and Jacquinot), *C. petrosa* (Wood), *C. purpurastoma*, new species, *C. inflata* (Quoy and Gaimard), *C. irrorata* (Gould), *C. nympha*, new name. Three subspecies, *C. bifasciata persica*, new subspecies, *C. petrosa chemnitziana* (Pilsbry), *C. petrosa gennesi* (Fischer and Vignal), and three fossil species, *C. verbeekii* (H. Woodward), *C. tjiolonganensis* (K. Martin), and *C. alasaensis* Wissema also are recognized.

THE EGG MASSES OF GASTROPODS FROM THE NORTHWESTERN RED SEA, A PROPOSED SCHEME OF THEIR CLASSIFICATION.

Gamil N. Soliman, Department of Zoology, University of Cairo, Giza, Egypt.

The egg masses of more than 50 species of prosobranch and opisthobranch gastropods from the northwestern Red Sea have been described. As in most trochids (and most archaeogastropods in general) eggs are emitted singly in *Trochus dentatus*. The majority of gastropods, however, possess spawn masses of various forms. Shapeless gelatinous masses are possessed by some Turbinidae *(Turbo radiatus)*, but these acquire a globular shape in some Trochidae *(Trochus erythraeus)* and some Sacoglossa *(Elysia olivaceus)*. Soft horny capsules are incubated in the mantle cavity of female coralliophilids. Hard vase-shaped capsules are stuck singly or in groups in the neogastropod Muricidae *(Chicoreus virgineus, Murex ramosus)*, Thaididae *(Thais savignyi)*, Fasciolariidae *(Pleuroploca trapezuim)* and Conidae *(Conus sp.)*. The archaeogastropod Neritidae *(Nerita forskali)* lay small flattened hard isolated capsules. Eggs may further be deposited in coiled gelatinous ribbons which are either sand covered with coils one above the other (naticids), laid flat in the same plane with coils around the preceding ones (some dorid nudibranchs: *Chromodoris quadricolor, C. inornata, Gymnodoris limaciformis, Phyllidia varicosa*), or are attached edgewise (most nudibranchs and some Sacoglossa: *Phyllobranchillus orientalis*). Gelatinous egg strings may be regularly coiled as in most aeolids *(Phyllodesmium xeniae)*, or long and much entangled: sand covered (Strombidae) or free of any deposits (most Anaspidea).

An attempt has been made to classify the egg masses of the gastropods studied as well as those of other gastropods (including the pulmonates) into common types instead of dealing separately with the spawns of either the prosobranchs, opisthobranchs or pulmonates. This method helps to avoid false typifying of spawn morphologies among the Gastropoda and reduces the major types to only four. A better understanding of the reproductive biology of gastropods could be achieved by studying other aspects of reproduction of the three subclasses together in the way followed with their egg masses.

SYSTEMATIC REVISION OF THAIDID GENERA BASED ON ANATOMY. **Silvard P. Kool,** The George Washington University, Washington, D.C..

The status and validity of the thaidid genera *Thais* (Roeding 1798), *Purpura* (Bruguière 1789), *Nucella* (Roeding 1798), and *Mancinella* (Link 1807) were examined by study of the type species of each genus (*T. nodosa, P. persica, N. lapillus, M. alouina,* respectively). Five other species presently allocated to these four genera were studied as well.

Due to a high degree of convergence in shell morphology and considerable intra- and interspecific variability in shell shape, only anatomical and radula characters were considered. Twenty-five characters were taken from the reproductive system, alimentary system, and mantle cavity, and nine from radular morphology. Phylogenetic relationships are proposed based on a cladistic analysis using the Wagner 78 program. A phenogram was obtained using the PHYSIS UPGMA analysis.

This study indicates a clear distinction between *Nucella* and *Thais*, both considered valid genera herein. The genus *Mancinella* likewise deserves full generic status. The genus *Purpura, sensu latu,* is not monophyletic; thus the older generic name *Purpurella* (Dall 1871) should be resurrected for the Caribbean species, *P. patula*.

FANCY FOOTWORK: FUNCTIONAL MORPHOLOGY OF THE FOOT OF THE LIGHTING WHELK *BUSYCON CONTRARIUM*. **J. Voltzow.** Duke University, Durham, North Carolina.

Gastropods crawl, leap, burrow, mate, and catch prey using a single, flexible foot. The foot of *Busycon* is composed of a complex network of blood vessels, muscle fibers, and connective tissue. Near the pedal ventral surface, blood is channeled through discrete spaces delimited by the muscle and connective tissue of the sole. This musculature consists of a three-dimensional interwoven network of collagen-wrapped muscle fibers. Recordings of intramuscular pressure from the feet of *Busycon* reveal specific patterns of pressure fluctuations that correspond to the behaviors of resting, crawling and burrowing. Each pattern is the result of muscles antagonizing muscles directly and indirectly via the blood-muscle-connective tissue continuum of the sole. The special features of this continuum are responsible for the flexibility of the gastropod foot.

HATCHING SIZE VARIATION IN *NUCELLA LAPILLUS* ALONG AN ENVIRONMENTAL GRADIENT OF WAVE EXPOSURE. **Ron J. Etter,** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

Embryonic development of many marine prosobranchs occurs within benthic egg capsules and the nourishment to sustain development is provided in the form of nurse eggs. Hatching size in these snails is dependent on the number of nurse eggs an embryo ingests during this period and is typically quite variable. Several hypotheses have been advanced to support the notion that interpopulation variation in hatching size is adaptive, although little direct evidence is available. One such hypothesis proposes that hatching size will be larger where environmental stresses are more severe. The intertidal snail *Nucella lapillus* was used to examine this hypothesis along an environmental gradient of wave exposure. Although the length and volume of egg capsules were similar among populations, the number of hatchlings emerging from capsules were positively, and their mean size negatively correlated with wave action. Intrapopulation variation in hatching size, in part, reflects differences in the number of embryos placed within egg capsules while variation between populations appears to result from differences in the number of nurse eggs deposited within capsules. Since shores protected from heavy wave action tend to experience more stressful conditions, both biotically and abiotically, these findings indicate hatching size varies in the predicted direction.

DIET AND THE CRYSTALLINE STYLE IN THE OMNIVOROUS NEOGASTROPOD, *ILYANASSA OBSOLETA* (SAY). **Lisa C. Hendrickson,** North Dartmouth, Massachusetts.

Temporal fluctuations in crystalline style wet weight and protein content were measured for the deposit-feeding omnivore, *Ilyanassa obsoleta*, to determine whether variations in style size are attributable to differential digestive responses, of mudsnails, to particular diets.

Mudsnails (12.0-14.0 mm) held in laboratory microcosms were allowed to feed, for one hour, on either a carrion or microalgal food source, following a five-day starvation period. A control group consisted of snails that remained starved throughout the experiment. Simultaneous measurements of style wet weight and protein content were collected for all three groups, and their corresponding normalized means were plotted over a 12-hour period.

Fluctuations in the mean style size of algae-fed snails reflected those of the control group, however, the mean style size of snails fed carrion did not change significantly during the experimental period. Further studies, which focus on the extracellular digestion of carrion, are being conducted.

SEASONAL VARIATION IN THE FREEZING TOLERANCE OF THE MARSH SNAIL *MELAMPUS BIDENTATUS*. **D. R. Hayes** and **S. H. Loomis,** Department of Zoology, Connecticut College, New London.

Melampus bidentatus survives harsh winter temperatures by allowing ice to form in its body fluids. This freezing tolerance is a seasonal mechanism that is present from late fall to mid-spring. The mean lethal temperature of the snail ranges from -13.0° C in December to -5.5° C in July, while the corresponding supercooling point of the hemolymph ranges from -7.4°C to -11.5°C. The winter hemolymph contains ice nucleating agents that promote extracellular ice fromation at high temperatures, preventing excessive supercooling and lethal intracellular ice. When heated at 100° C for 5 minutes, the winter hemolymph lost all nucleating activity. Dialysis for 24 hours caused no change in supercooling temperature, and indicated that the molecular weight of the nucleator was greater than 12,000 to 14,000. Treatment with a non-specific protease decreased the supercooling point, but the change was not significant. A 1% solution of hemolymph and distilled water raised the supercooling point of the water significantly. These data indicated that an ice nucleating agent is produced in the hemolymph in the winter and degraded in the spring, and is probably proteinaceous.

FUNCTIONAL IMPORTANCE OF THE PALLIAL EYE OF *CERITHIDEA SCALARIFORMIS*. Thomas N. Rogge, Department of Biological Sciences, University of Southern Mississippi, Hattiesburg.

A preliminary study was done to investigate the differences between the pallial and cerebral eyes of the marine mesogastropod *Cerithidea scalariformis*. Of particular interest was the function of the pallial eye, which fits into the siphonal notch of the shell aperture and is visible through a transparent spot in the operculum. *C. scalariformis* is considered amphibious, spending a great amount of time suspended from marsh grasses by mucous threads. When feeding, the snail's head is buried in the bottom detritus, leaving only the pallial eye unobstructed. Histologically, the different eyes reflect behavioural differences in the snail. Using simple light/dark preference tests, it was found that snails with pallial vision (cerebral eyes removed) behaved similarly to snails with complete vision (all eyes intact), whereas snails with cerebral vision (pallial eyes removed) behaved oppositely to snails with complete vision. From experimental results and field observations, I suggest that the pallial eye has twofold importance: orienting and directing the snails movements and to "watch" for possible predatory dangers both while feeding and suspended from grasses. Both in the field and laboratory, the snail will dislodge itself and fall from its suspended perch or withdraw into its shell while feeding if passed closely by. It is possible that this is a reaction to moving shadows of potential predators.

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EXPLORATION FOR COMMERICAL QUANTITIES AND MARKETS FOR BLOOD ARKS. Arnold G. Eversole, Department of Aquaculture, Fisheries and Wildlife, Clemson University , Clemson, **William D. Anderson** and **Will H. Lacey**, Office of Fisheries Management, South Carolina Wildlife and Marine Resources Center, Charleston, South Carolina.

Eighteen hydraulic escalator cruises were made in 1983 and 1984 to assess the potential for commercial exploitation of blood arks along the coast of South Carolina. Commercial concentrations of *Noetia ponderosa* and/or *Anadara brasiliana* were located in 7 of 27 areas sampled. *N. ponderosa*, the most abundant species, was found in high salinity waters behind coastal barrier islands with populations of *Mercenaria mercenaria, Chione cancellata* and *A. ovalis*. The second most abundant ark, *A. brasiliana*, was found frequently 1/4-1/2 nautical miles offshore of barrier islands in sandy substrata, sympatrically with *Polinices duplicatus*. *A. ovalis*, the true blood ark, was third in abundance and usually found with *N. ponderosa*. *A. transversa* was rarely caught and never in commerical concentrations. *N. ponderosa* was the largest ark and had the heaviest shell of the species assessed. *A. ovalis* had the smallest mean shell length and the lowest meat yield (meats per pound). Ark meats contained considerable water (83%) and protein (68% on a dry weight basis).

Hydraulic escalator harvesters with Maryland-type heads were evaluated in offshore and estuarine waters for harvesting arks in subtidal waters. This gear proved most effective in estuarine areas at depths less than 8.0 meters.

Questionnaires containing valves of the three most abundant species were sent to seafood dealers in 10 countries including the United States. Responses to questionnaires indicated that 50% of the dealers were familiar with these species and 80% reported a similar species in their market. Other responses to questions about product marketability and price indicated little potential for exporting these species to foreign markets. This may be due in part to the fact that *A. granosa* and *A. broughtonni* are abundant in the Far East. Responses from domestic seafood dealers also indicated there was no viable market for blood arks at this time.

THE EVOLUTION OF LIGAMENT SYSTEMS IN THE BIVALVIA. T. R. Waller, National Museum Of Natural History, Smithsonian Institution, Washington, D.C.

Ligament systems (arrays of fibrous and nonfibrous ligaments and their supports) were surveyed throughout the Bivalvia with particular attention to structure, ontogeny, paleontology, and taxonomic distribution. New observations indicate that the primary ligament system was opisthodetic but that the inner ligament layer contained aragonitic granules, not fibers as in modern fibrous ligament. A vestige of such a system remains in modern Nuculacea.

Primitive opisthodetic ligament systems, termed *simple arched or planar systems*, rest on the unmodified inner surface of the shell without nymphae and may or may not be arched depending on the relative thickness of fibrous and nonfibrous ligaments. Among modern bivalves such systems are limited to the Nuculanacea (where they are typically developed in the Malletiidae) and the Nucinellidae in the Solemyoida.

Other ligament systems can be derived from simple arched or planar systems by means of two morphological events which occurred independently, producing two major clades. One event was the development of nymphae, ridges formed from the inner surface of the shell which serve to enhance arching. Nymph-bearing systems, to which the term *parivincular* is restricted, are exclusively opisthodetic and occur in the Solemyidae and throughout the subclasses Anomalodesmata, Paleoheterodonta, and Heterodonta. The other event was the development of *pseudonymphae*, which consist of modified ostracum and serve as fillers between ligaments and shell. Pseudonymph-bearing systems, termed herein *planivincular*, are exclusively opisthodetic and are taxonomically restricted to the subclass Isofilibranchia. Planivincular systems are also characterized by discontinuous ontogeny of fibrous ligament, the initial portion being a tiny fibrous resilium. In *Dacrydium*, only this early part remains, the remainder of the ligament system being truncated by neoteny. Multivincular and duplivincular systems can be derived from planivincular systems by similar truncation and by the reestablishment of adult ligament systems through repetition of either fibrous or nonfibrous ligament. The Pectinacean ligament system, with its unique centrally nonfibrous resilium, would appear to be derived from a duplivincular system.

The parivincular clade originated by middle Ordovician time in forms such as *Ctenodonta nasuta* (Hall). The planivincular clade likely originated from the Protobranchia even earlier.

SHELL MICROSTRUCTURAL VARIATION REFLECTS HABITAT INFLUENCE IN *GEUKENSIA DEMISSA GRANOSISSIMA* (BIVALVIA: MYTILIDAE). **Antonieto Tan Tiu,** University of Southern Mississippi, Hattiesburg, Mississippi.

Live specimens and freshly shucked shells of the Atlantic ribbed mussel, *Geukensia demissa granosissima*, transplanted to a continually submerged habitat (Winter 1985, Ocean Springs, Mississippi) showed an internal shell growth layer different from that of mussels of higher *Spartina alterniflora* Loiseleur-Deslongchamps salt marsh. The high salt marsh was alternately exposed to air and submerged in water (about 50% of total experimental period), while submerged habitat was continuously submerged in water. Shell lengths significantly decreased in emerged mussels (high marsh) and increased in submerged mussels (submerged habitat). Scanning electron microscopy observation of the internal shell microstructure inside and outside the pallial line of both anterior and posterior regions of initially collected (baseline) and caged mussels (live and freshly shucked shells) revealed that (1) Inside the pallial line, the nacreous layer was predominantly eroded in all mussels; a homogeneous-like microstructure composed of variously shaped and sized particles occurred in all mussels but submerged. (2) Outside the pallial line, growing and mature tablets with smooth surfaces were observed in both baseline and submerged mussels but not emerged mussels. Few emerged mussels had elevated borders of continuous ridges, beads or granules that surround partially or completely one or more tablets. These circumferential ridges may be due to shell dissolution rather than shell formation. In conclusion, distinct differences in internal shell microstructure occurs in mussels maintained between different habitat within a very small area. Submerged regions, at least in the winter season of the Mississippi Gulf Coast, may offer some buffering capacity to climatic variation and thus increase the ability of *G. d. demissa* to deposit shell material or deter shell dissolution.

INTENSE PREDATION BY CRABS ON MANGROVE LITTORINIDS. **David G. Reid,** Department of Invertebrate Zoology (Mollusks), National Museum of Natural History, Smithsonian Institution, Washington, D.C.

A taxonomic revision of the *"Littorina scabra"* group in the Indo-Pacific using characters of the shell and anatomy, has defined 17 species, which are placed in the genus *Littoraria*. Five of these species occurred at a study site on Magnetic Island, Queenland, where they were zoned at characteristic heights above the water level on *Avicennia* and *Rhizophora* trees.

From field observations and laboratory experiments, the major predators of post-larval snails were concluded to be grapsid crabs of the genus *Metopograpsus*, and the portunid *Thalamita crenata*. The grapsids were small, tree-climbing crabs with unspecialized chelae, capable of crushing small or thin-shelled snails. The portunid was a large species with dimorphic chelae, able to crush even the largest *Littoraria* species, but could only reach prey close to the water surface. From exclusion cage experiments in the field using *L. filosa*, it was estimated that crabs caused 79% of the mortality of snails in the size range 7 to l2 mm.

Repaired V-shaped breakages on the shell preserve a record of unsuccessful predation attempts by crabs during the life of a snail. Frequencies of repaired breakages in the *Littoraria* species were very high (means of 0.66 to 3.48 repairs per shell). From the known growth rates of the species, rates of injury were calculated, and found to be highest at small shell sizes (< 5 mm for most species). The size at which the rate of injury was highest corresponded to that at which snails just achieved immunity to the majority of *Metopograpsus*.

The *Littoraria* species zoned at lower levels on the mangrove trees had thicker shells, which can be explained as an adaptation to the increased severity of crushing predation nearer the water level.

CONTRIBUTIONS OF ALPHEUS HYATT TO MALACOLOGY. **Ralph W. Dexter,** Kent State University, Kent, Ohio.

Alpheus Hyatt (1838-1902) was trained by Louis Agassiz, and served as Honorary Curator of Fossil Cephalopods at the Museum of Comparative Zoology for life (1865-1902). He was also part-time Curator of Conchology (1863-67) and Curator of Paleontology (1867-70) at the Boston Society of Natural History, and Curator of Lower Invertebrates at the Peabody Academy of Science, Salem, Mass., before returning to the Boston Society of Natural History (1870) as Museum Custodian (i.e. Curator) for the remainder of his career. He founded the Teachers School of Science and the Annisquam Seaside Laboratory (which became the

Marine Biological Laboratory at Woods Hole). With his private vessel he conducted dredging studies off the New England coast and made expeditions to Anticosti Is. to collect marine specimens and fossil cephalopods. He published some 50 papers on fossil cephalopods, describing many new genera and species (See *Malacol. Rev.* 6:38-40. 1973).

While studying mollusk collections in European museums (1872-73), he did special research on fossil planorbid shells and their supposed evolution at Steinheim (Germany) leading to a monograph (1880). He was a cofounder with E.D. Cope of the Neo-Lamarckian school of evolution and developed a theory of growth and development later called the Hyatt-Cope theory of acceleration and retardation. Hyatt also proposed an "old age theory" attempting to explain the life history of species. His last study — never completed — was on the geographical distribution and color patterns of land snails in Hawaii (Achatinellidae).

THE MARINE MOLLUSKS OF THE BAHAMA ISLANDS: IDENTIFICATION SYSTEMATICS, ZOOGEOGRAPHY, AND NATURAL HISTORY. Robert Robertson, Academy of Natural Sciences, Philadelpia, Pennsylvania.

This book is being prepared in collaboration with Jack N. Worsfold and Colin Redfern. About 1,300 species will be treated. The intended readership is serious amateur shell collectors, and marine malacologists and biologists. Currently, we are working on the introduction and archaeogastropods. We summarize here the most important background information in the introduction.

The Bahamas are limestone islands on slowly subsiding shallow banks stretching about 1000 km SE of S Florida, N of the West Indies. At their margins, the banks slope gently to depths of about 30 to 40 m, below which, surrounding all the banks, there is a nearly vertical "drop-off" to much deeper water. During each glacial advance in the Pleistocene, world sea level fell. This happened most recently only 20,000 to 15,000 years ago, when it fell somewhere between 85 and 130m (Milliman and Emery, 1968; CLIMAP Project Members, 1976; Emiliani, 1980). The Bahamian banks must have become towering plateaus surrounded by cliffs.

Presently, mean near-surface sea temperatures are 24° (winter) and 28° C (summer) (Fuglister, 1947). In Tongue of the Ocean (the deep-water embayment between Andros and New Providence) during each glacial advance temperatures have been estimated by Lynts *et al.* (1973) to have been 3° or 4° C lower than at present, perhaps enough to have eliminated some stenothermal species.

During each glacial advance, most of the non-rock-dwelling marine biota must have been exterminated. Habitats and organisms that we believe to have disappeared totally are: sand, turtle grass (*Thalassia*), mud, mangroves (*Rhizophora*, etc.), and most holothurians. Most of the now rich fauna in these habitats must have repopulated the Bahamas in the last 15,000 years. (The repopulation possibly happened much more quickly than this.) The source of the larvae would have been the West Indies, islands where the submarine geomorphology is different and whence currents flow. Bahamian habitats and organisms that may have persisted despite the low sea levels are supratidal to subtidal rock surfaces, remnants of coral reefs, gorgonians, zoanthids, sponges, floating *Sargassum*, *Janthina*, plankton, nekton, and deep-sea taxa.

On average, 1.7 tropical storms and hurricanes pass through or seriously affect the Bahamas each year (Halkitis *et al.*, 1982). The shallow water biota is temporarily devastated in their paths.

Seven Bahamian gastropods with direct development were known to D'Asaro (1970). Examples are *Fasciolaria tulipa* (Linnaeus, 1758) and *Turbinella angulata* (Lightfoot, 1786). There are no doubt more. (Non-neritacean archaeogastropods were believed by Strathmann (1979) all to be lecithotrophic, but this generalization may not be true.) It is puzzling how species with nonplanktonic larvae populated the Bahamas, but the Great Bahama Bank is separated from the Cuban "continental" shelf by the Old Bahama Channel, which at its narrowest is only about 10 km wide. Furthermore, some far more isolated tropical islands have nonplanktonic species in their faunas.

An example of a marine mollusk species apparently endemic to the Bahamas is *Vexillum (Pusia) chickcharneorum* Lyons and Kaicher (1978), but this, like the others, may turn out to occur also in the West Indies. A species possibly extinct in the Bahamas is *Cancellaria reticulata* (Linnaeus, 1767), occurring there in Pleistocene deposits (it persists outside the Bahamas).

One school of ecologic thought has it that tropical biotas, with their many species, have fairly stable populations. Our findings support the alternative view: because of extrinsic and probably also intrinsic factors, there is frequent decimation and resurgence of populations.

A PRELIMINARY BIOGEOGRAPHY OF THE BULIMULIDAE (PULMONATA: SIGMURETHRA) IN SONORA MEXICO. J.E. Hoffman. University of Arizona, Tucson.

Pulmonate snails in the deserts of the southwestern United States and northern Mexico usually display a patchy distribution wherein small populations are often totally isolated from one another. This generally results in the evolution of many species, often one or two per mountain range or patch of habitat. This has been shown to be the case for the genus *Rabdotus* in Baja California as well as *Sonorella* in Arizona and Sonora.

Preliminary research indicates, however, that this is not the case for *Rabdotus* in Sonora where only two species appear to inhabit hundreds of square kilometers of patchy habitat, with only a few related species which inhabit very limited ranges within or adjacent to the ranges of the two major species. This pattern, while unusual for desert land snails, is not unusual for *Rabdotus*; this pattern occurs often in this genus further east.

Of the two widespread species, *R. nigromontanus* seems to occur in and around Sonora's major river basins, and the almost continuous good habitat along these basins seems to provide a means for gene flow within most of the species' range. The other species, *R. baileyi*, inhabits lower, much more xeric habitats with no permanent rivers. Within its range, *R. baileyi* inhabits isolated rock outcrops. A means by which gene flow might be maintained in this species is being sought.

In addition, a member of the genus *Orymaeus* in this family was found in the southern part of Sonora, a new record for this state.

INFLUENCE OF OPTIC TENTACULAR PRINCIPLE IN THE BIOSYNTHESIS OF STEROIDS IN THE OVOTESTIS OF *CRYPTOZONA BELANGERI* (DESHAYES) (PULMONATA;GASTROPODS).

S. Rajasekaran, V. Sriramulu and **T. Sridharan,** Department of Zoology, Annamalai University, Annamalainagar, India.

Isoprenoid lipids, as components of hormones, are indispensable in the physiology of reproduction, since they regulate the functional differentiation of the reproductive organs during reproduction. Progesterone, testosterone and estrogen are groups of 21, 19, and 18 isoprenoid lipids which play an important role in regulating the reproductive activity in animals. The occurrence of the intermediary structure 17-b hydroxy testosterone in the pathway of conversion of estrogen from testosterone has also been studied, along with the progesterone, testosterone and estrogen in the gonad of the terrestrial pulmonate gastropod mollusc *Cryptozona belangeri* (Deshayes) using low frequency H'FT NMR Spectrometer.

The experimental snail is protandrous hermaphrodite where the male reproductive organs are activated first after the differentiation of the gonad towards the male phase (spermatogenesis) followed by the female phase (oogenesis). The spectrographic pictures showed that the male phase gonad has a higher level of testosterone, the estrogen level being low and while the female phase gonad exhibited a higher level of estrogen together with an increased level of 17-b hydroxy testosterone. The spectrographs of the optic tentaculamised male phase snail analysed at an interval of 10 days up to 30 days showed a sharp fall in the titre of testosterone level, but recorded a characteristic increase in the level of estrogen. The 17-b hydroxy testosterone signalled an initial increase followed by a fall within 20 days after tenetaculectomy paving the way for the enhanced biosynthesis of estrogen.

In the present investigation, it is inferred that the steroid hormones are synthesised in the ovotestis of the snail and the hormones elaborated characterize the specific sex in the hermaphroditic snail, either to conform to male or female phase. The results of the optic-tentaculamised snails illustrate the prevalence of relationship of optic tentacle with the gonad. Switching over from one phase to the other phase depends on the optic tentacular principle which plays a decisive role in modulating the biosynthesis of specific steroids, either androgens or estrogens, by gonad characterising the male or female phase of the snail.

RADULA DYNAMICS: ANALYSIS OF MOVEMENT PATTERNS AND SUBSTRATE INTERACTIONS.

Carole S. Hickman, Department of Paleontology, University of California, Berkeley.

The morphological complexity of the molluscan radula makes the structure a rich source of characters for taxonomic differentiation and analysis of phylogenetic relationships. The radula is also a source of "unconventional" characters that are derived not from static morphology but from analysis of radular function. Changes in spatial relationships of teeth, sequences of individual tooth-tooth interactions and tooth-substrate interactions, paths and rates of tooth movement, as well as patterns of tooth row movements and interactions are more variable than the static morphology of the extracted radula and its individual teeth.

Two techniques for defining dynamic characters are motion analysis of filmed feeding strokes and analysis of feeding tracks on artificial and natural surfaces.

Frame-by-frame analysis of a single feeding stroke of a duration of one second and filmed at 64 frames/second provides 64 static images of successive positions of tooth rows and individual teeth. Traces of the motion of rows and individual teeth relative to fixed points on the substrate yield patterns that can be described, illustrated, and quantified in the same ways that conventional morphology is treated. This method of analysis is restricted to animals that can be induced to protract and retract the radula on a transparent surface for filming. Feeding track analysis can be used alone or in conjunction with dynamic analysis. The traces of teeth on artificial and natural substrates have their own static morphology and also can be described, illustrated, and quantified in the same manner as conventional characters. If relationships can be established between individual incisions and the teeth that produced them and if the temporal sequence of incisions can be established, then several higher levels of pattern are available for use as characters. The four temporally and spatially parallel gouges of a patellacean limpet provide a striking contrast to sets of spatially parallel but temporally sequential gouges of a trochacean gastropod. When the traces are oriented relative to a morphological constant (the longitudinal axis of the radula) the difference is even more striking because the longitudinal axes of the gouge sets are 90 apart.

Traditional systematics avoids the use of functional and behavioral characters on the grounds that common function and behavior frequently are the result of convergence. However, if function is precisely defined and expressed in terms that are essentially morphological, it extends the definition of form and provides a basis for unmasking convergence in static morphology.

FUNCTIONAL MORPHOLOGY OF SOME CHITONID RADULAE (POLYPLACOPHORA: CHITONIDAE).

Robert C. Bullock, Department of Zoology, University of Rhode Island, Kingston.

The radula of the polyplacophoran family Chitonidae consists of 17 highly modified teeth per row. There is much within row and within column integration of tooth function and the rows are difficult to discern due to their offset nature. Each centro-lateral of *Chiton* and *Acanthopleura* has a single cusp with a small pad on the distal lateral edge that articulates with the shaft of the major lateral when the ribbon is curled. The use of magnetite on the denticle cap of the major lateral is usually conserved and its presence on the back surface of the self-sharpening cusp is limited to the outer margin and a pronounced central tab that possibly protects the cap during withdrawal. When the ribbon is curled the wings of opposing major laterals meet and prevent the denticle caps from abrading each other. The wings may also aid in the collection of food particles.

Each major lateral articulates with at least two inner small laterals. The outer small lateral helps to support the major uncinus which often has an L-shaped base. The inner marginal also supports the major uncinus and directs it inward during the curled position such that the distal blade interleaves two denticle caps. The major uncinus shields the unprotected back surface of a denticle cap from contact with the heavily mineralized portion of the next denticle cap in the column, but it also appears to serve as a sweeping tooth to collect food particles.

Near the anterior end the radula ribbon expands laterally and the denticle caps are directed inward. When *A. granulata* feeds 3-6 pairs of major laterals converge medially. The conspicuous grazing marks are roughly perpendicular to the longitudinal axis of the animal and they do not meet at the center. This indicates that this species probably rasps small particles from the substrate, but it is incapable of tearing away larger pieces.

RADULAR EVOLUTION IN THE PATELLOGASTROPODA.

David R. Lindberg, Museum of Paleontology, University of California, Berkeley, California.

The Patellogastropoda (families Patellidae, Acmaeidae and Lepetidae) have a unique radula morphology among the Gastropoda. The bending plane over the odontophore is flat rather than curved as in other gastropod taxa and thus the radular teeth interact with the substrate like a rasp rather than being splayed against it. The lateral teeth are impregnated with ferrous oxides, and are positioned in either a stepped arrangement (the inner laterals are in a row) or inverted V arrangement (the lateral teeth diverge posteriorly). All three families have similar lateral tooth modifications for particular food types. Modifications for coralline algae, fleshy marine plants, and high intertidal flora are remarkably similar between families. Basal plate morphology becomes more complex in the derived taxa (*Patella* ➧ *Cellana* ➧ acmaeids). Evolutionary trends in the patellogastropod radula include: (1) the derivation of the inverted V configuration from the stepped configuration, (2) the reduction of tooth number, (3) the development of basal plates, and (4) the modification of lateral teeth for specific habitats. Simple changes in radular development appear to be responsible for the various radular configurations in the patellogastropods. The developmental events include the failure of odontoblasts to divide and the fusion of odontoblasts. Teratological radulae suggest that these events occur in three distinct tooth fields. The bending plane of the radula over the odontophore, the stepped radular configuration, and the presence of ferrous oxides in the lateral teeth are also present in polyplacophoran and monoplacophoran taxa.

AQUATIC MOLLUSCA OF THE ARKANSAS RIVER BASIN.

Mark E. Gordon, Department of Zoology, University of Arkansas, Fayetteville.

The Arkansas River drainage with a 416,071 km^2 watershed is a major tributary system within the Interior Basin. Arising from the Continental Divide in Colorado, the Arkansas River flows 2333 km and descends 4366 m through several geomorphic provinces to its confluence with the Mississippi River. The aquatic malacofauna of the Arkansas basin has been assessed from critical review of published surveys, examination of museum vouchers, and personal collecting. One hundred three species have been identified: 37 gastropods, 50 unionaceans, and 16 sphaeriaceans. Six species have been introduced and another five unionaceans may exist in the faunally little-known portion within the Mississippi Alluvial Plain.

While the fauna is primarily composed of wide-spread Interior Basin species, high species richness has developed due to interactions between diverse physical conditions and regional endemism. Rocky Mountains habitats are dominated by rather ubiquitous, pioneering pulmonates and pisidiids. Similar faunal composition extends across the xeric High Plains. Influx of species, including unionaceans, occurs as the river flows into the more mesic Central Lowlands. Species richness is maximized near the junction of this province and the Interior Highlands. In this area, environmental parameters are most diverse and distributions of northern and southern Interior Basin species and Interior Highlands endemics are sympatric. As a result, several northern species reflect disjunct distributions relative to the rest of their range. While stream capture has been speculated as the explanation for such, these patterns are probably artifacts of Pleistocene biogeography. Post-Pleistocene climates restricted these northern species to upper portions of the drainage while southern species were able to invade Central Lowlands habitats via the conduit through the Interior Highlands represented by the low-gradient Arkansas River. Such southern recruitment may have been enhanced by the former channel of the extreme lower Arkansas which is presently occupied by Bayou Bartholemew.

DIURNAL AND SEASONAL VARIATION OF TERTIARY DIGESTIVE TUBULE MORPHOLOGY IN *CORBICULA FLUMINEA* (MÜLLER).

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Digestive tubule morphology during 24-hour periods in *Corbicula fluminea* show that animals maintained and sampled in the laboratory and those that were field sampled show different tubule appearance. "Starved" laboratory animals showed more random tubule morphology. "Fed" laboratory animals showed dominance of tubules in disintegrating and absorptive stages. Field sampled animals also show dominance of disintegrating and absorptive stages. Tubule morphology of bivalves in field samples and "fed" laboratory animals throughout 24-hour periods suggest continuous feeding. There is however, a notable difference in digestive tubule appearance between field and "fed" laboratory animals. Within digestive cell cytoplasm of field animals were found varying degrees of excretory vacuole formation. These vacuoles varied in size, position and amount of particulate material inside. For the purpose of interpreting field data, digestive tubule appearance was categorized into three types. The first type, designated as type A, were tubules that had digestive cells devoid of observable excretory vacuoles under light microscopy. Type B were tubules that digestive cells had vacuoles of small size located in a proximal position with or without particulate matter inside. Type C tubules had cells with large vacuoles in a central or distal position with particulate matter. Percent of bivalves with type A, B or C tubule type within each hourly field sample ($n = 20$) taken three times between September 1984 and August 1985 was used to determine possible rhythms of intracellular digestion. Evidence suggests that feeding and digestion in the bivalve, although continuous, is modified by light intensity. Bivalves with highly vacuolated digestive cells were dominant during daytime in September. In June and December samples however, no clear dominance of any of the three tubule types was found for the 24-hour period.

FUNCTIONAL MORPHOLOGY OF THE MANTLE OF NORTH AMERICAN CORBICULACEA. G.L. Mackie, Department of Zoology, University of Guelph, Ontario, Canada.

The mantle edges of twenty-one species of freshwater Corbiculacea were examined for differences in morphologies of mantle folds to determine their taxonomic value and functional significance. The only apparent familial feature is the presence of three distinct distal folds in the mantle edge of Corbiculidae and two in Pisidiidae. Within the Pisidiidae the relative lengths of the middle and outer mantle folds and the presence or absence of cilia and the extent of ciliation on the inner fold appear to be of taxonomic value at the species level. The cilia probably help to circulate water in the mantle cavity, especially in species characteristic of standing waters.

ASPECTS OF COMPARATIVE EMBRYOGENESIS IN THE PISIDIIDAE AND THE CORBICULIDAE (BIVALVIA: CORBICULACEA). Louise Russert-Kraemer, Marvin L. Galloway and **Mark E. Gordon,** University of Arkansas, Fayetteville.

Microscopical serial sections and freeze-cracked SEM sections were prepared and examined to work out aspects of the comparative embryology of *Corbicula fluminea, Sphaerium striatinum* and *Pisidium casertanum,* and to investigate events of developmental "timing" in representative species of corbiculid and pisidiid bivalves. Earlier evidence of heterochrony in *C. fluminea* (Kraemer and Galloway, 1984) was confirmed. Retention of trochophore, pediveliger, veliger, early straight-hinged juvenile and late straight-hinged juvenile stages in *C. fluminea* within the marsupial gill, contrasts strongly, for example, with their suppression in *S. striatinum.* In *S. striatinum* freeze-cracked SEM clearly reveals that developmental stages are compressed from gastrula to juvenile; that the juvenile is retained and attached by its placental byssus to the marsupial gill wall, until it attains a size and degree of tissue differentiation very closely approximating that of the parent. SEM confirms an observation made earlier by Mackie, that the "placenta" is *not* a "placenta." It is exclusively a connective tissue outgrowth of the embryonic foot which constitutes a broad, strong, non-vascular holdfast attachment to the marsupial gill wall. It appears that production of the byssal holdfast and its attachment constitute the critical embryonic events for pisidiid bivalves, which allow them to veer away from the more marine/estuarine bivalve-like developmental timing preserved in the embryogenesis of *C. fluminea*.

SPAWNING PERIODICITY OF THE ASIATIC CLAM, *CORBICULA FLUMINEA*, IN THE NEW RIVER, VIRGINIA. F. G. Doherty, D. S. Cherry and **J. Cairns, Jr.**, Department of Biology and University Center for Environmental Studies, Virginia Polytechnic Institute and State University, Blacksburg.

Three approaches were utilized weekly to assess the spawning periodicity of the Asiatic clam, *Corbicula fluminea,* in a flow regulated reach of the New River, Virginia, for the duration of the 1984 reproductive season. Data were collected on the number of newly recruited larvae in the New River sediment, number and life stage of larvae naturally released from adults held in a laboratory invertebrate culture device, and the degree to which adult brood chambers were charged with developing larvae for which indices were calculated. Periodicity and relative intensity of spawning effort as determined by each approach were generally compatible. These comparisons reveal three major peaks in spawning activity occurring in June to early July, late August, and early October, each from 2 to 6 weeks duration.

Larval sediment concentrations (number per meter^2) peaked seasonally at 16,000, 18,000, 14,000, and 18,000 for the collection days of June 12, July 17, September 4, and October 2, respectively. Larval releases from laboratory held adults peaked seasonally with 1,900 and 1,800 larvae counted per adult for the weeks of June 26 and July 10, respectively, 1,050 for the week of August 21, and 1,275 for the week of October 2. Seasonal peaks in brooding indices occurred for the weeks of July 10 and October 2 with values of 3.5 and 2.7 (of a maximal value of 4.0), respectively. Midsummer index values never exceeded 1.8 (August 7 and 21, September 4). Spring and fall spawns coincided with rapidly rising and falling water temperatures, respectively. Mid-summer spawn occurred during a period when temperatures were relatively stable and never exceeded 26.1 C. These observations do not coincide with previously reported patterns of reproductive efforts by *C. fluminea,* suggesting that reproductive activity and spawning may be highly site specific.

UNIQUE SHELL MICROSTRUCTURE OF *CORBICULA FLUMINEA*. Robert S. Prezant and **Antonieto Tan Tiu,** Department of Biological Sciences, University of Southern Mississippi, Hattiesburg.

The internal shell edge (beneath the periostracal infolding) of the Asiatic bivalve *Corbicula* c.f. *fluminea* Müller frequently shows a unique spiral form of crossed-lamellar microstructure. Most populations we have examined from Mississippi show conical blocks of spirally arranged lathes that taper towards the shells exterior. These spirally arranged blocks are usually associated with high concentrations of conchiolin.

The orientation of the spiral cones suggests that they can help inhibit chipping along the shell edge by certain predators. Aside from function, this is the first report of spirally oriented crossed-lamellar microstructures in molluscs. At this point we have not found similar microstructures in any other corbiculid bivalve (incl. *Polymesoda caroliniana* and the "purple" form of North American *Corbicula*).

NOTES ON THE HISTORIC AND PRESENT NAIAD FAUNA OF THE CANEY FORK RIVER, CENTRAL TENNESSEE.

John E. Schmidt, West Virginia Department of Natural Resources, Charleston.

A survey of the naiad fauna of the Caney Fork River was conducted from August 1980 to August 1981 as part of planning for the Old Hickory Lake and Center Hill Lake projects. This work was performed for the Nashville District of the U.S. Army Corps of Engineers. Five locations were surveyed by first walking the banks and shoals looking for washed up shells. Shallow areas were searched with the aid of a water scope. In deeper water, naiads were located with a long-handled dredge. All relic and fossil shells were kept, cleaned, and sent to either Ohio State University or the University of Tennessee for identification or verification. Live naiads were identified and returned to the stream bottom.

A total of 36 species were represented in collections of relic and living naiads. The majority (28 species) were found only as relic or fossil shells from middens. The federally endangered species *Dromus dromas, Epioblasma florentina,* and *Pleurobema plenum* were collected as relic shells only. *Magnonaias nervosa, Amblema plicata, Fusconaia subrotunda, Elliptio crassidens, Elliptio dilitata, Potamilus alatus, Ligumia recta,* and *Lampsilis teres* form *teres* were collected alive.

Living naiads were collected infrequently no doubt due to their relatively low numbers in the Caney Fork River. The naiad fauna of the lower 27 miles of the river has not adapted to the combination of daily flow fluctuations (200 to 2000 cfs), cold water temperatures (hypolimnetic discharge), and nutrient poor water being released by the Center Hill Dam for peak electrical power generation. If one accepts 36 naiad species were once found alive in the river then a 78 percent reduction of the historic naiad fauna has occurred.

GAMETOGENESIS IN THREE HETEROGENERIC UNIONIDS (PELECYPODA: UNIONIDAE).

M. B. Kotrla. Department of Biological Science, Florida State University, Tallahassee.

The seasonal gonadal cycles of *Anodonta imbecilis* (Anodontinae), *Elliptio icterina* (Pleurobeminae), and *Villosa villosa* (Lampsilinae) were compared histologically and histochemically. These species were selected because they are bradytictic, tachytictic, and horotictic respectively and because they belong to subfamilies which were distinguished from one another on the basis of reproductive characters (Heard and Guckert, 1970, *Malacologia* 10:333-355). Specimens were collected monthly from a single site in Lake Talquin, Leon County, Florida for one year.

Neither the *E. icterina* specimens nor the *V. villosa* specimens are hermaphroditic. The female hermaphrodites of *A. imbecilis* have separate spermatogenic and oogenic acini. Four stages of gonad activity are observed: active gametogenic, ripe, spawned, and preparatory. The criteria by which these stages are distinguished are the degree of gamete maturation, the thickness and cell composition of the acinar epithelium, and the presence/absence of phagocytic cells in the acini. The time of year during which each stage occurs differs among species; within each species, spermatogenic and oogenic acini are not entirely synchronous.

Although sexual differences exist, there are no interspecific differences in the morphology and histochemical reactions of acini at any given stage. During active gametogenesis, immature gametes (gonial cells, young oocytes, spermatocytes) are found at the periphery of the empty acinar lumina. Acini in the ripe stage are filled with mature gametes; few immature forms are present. After spawning, a few gametes remain in each acinus and the acinar epithelium is at its thinnest. During the preparatory stage the acinar epithelium thickens to its yearly maximum. Residual gametes are phagocytosed by amoeboid cells which migrate across the epithelium. In spermatogenic acini, there are multinucleated cells, termed sperm-morulae, which have been reported to give rise to sperm (Heard, 1975, *Malacologia* 15:81-103). The origin and fate of these structure have yet to be confirmed.

THE MECHANICS OF GLOCHIDIAL ATTACHMENT (MOLLUSCA: BIVALVIA: UNIONIDAE).

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Glochidia are third class levers in which the valves form the lever arms and the single adductor muscle produces the in force. In this study the dimensions of the in and out lever arms, and adductor muscle were found and the position of the adductor muscle located for 35 species of unionid glochidia. From these data and an analysis of the possible configurations of adductor muscle and valve dimensions, it was determined that a majority of the glochidia within the Anodontinae and the Lampsilinae take advantage of the mechanical benefits of their structure to maximize speed of glochidial valve adduction by possessing long out lever arms (*Anodonta, Anodontoides, Alasmidonta marginata, Lasmigona complanata, Lasmigona costata, Ptychobranchus, Obovaria, Leptodea, Potamilus, Villosa, Lampsilis* and some *Epioblasma*). Other glochidia have developed means to maximize force of glochidial valve adduction at the expense of speed, by the use of large diameter adductor muscles and short out lever arms (*Alasmidonta viridis, Lasmigona compressa, Strophitus undulatus undulatus* and *Strophitus undulatus tennessensis*), or by the use of large diameter adductor muscles, long in lever arms and short out lever arms (*Pegias* and most *Epioblasma*). The Ambleminae were also found to have evolved the mechanics for speed of glochidial valve adduction by the use of long out lever arms (*Tritogonia, Quadrula pustulosa pustulosa,* and *Amblema plicata plicata*). However, strength was maximized by the use of long lever arm alone (*Magnonaias nervosa*) or by the use of long in lever arms and short out lever arms (*Quadrula cylindrica cylindrica,* and *Fusconaia ebena*) although it is suggested that this is accompanied by disadvantage in the form of reduced gape. This study suggests that the mode of glochidial attachment, whether for speed or strength, has played a large part in glochidial morphology and has produced convergence in valve shape as well as in the location, orientation and size of the glochidial adductor muscle.

PRELIMINARY STUDIES OF DEGROWTH PHYSIOLOGIES IN THE FRESHWATER PULMONATE SNAILS, *HELISOMA TRIVOLVIS* AND *HELISOMA ANCEPS*.

Jonathan Kyung Ho Han and **Jay Shiro Balboni-Tashiro,** Kenyon College, Gambier, Ohio.

A number of studies have examined the physiology and tissue biomass changes in overwintering specimens of the freshwater pulmonate *Helisoma trivolvis* . These studies have included assessments of animals overwintering in the field and maintained under simulated winter conditions in the laboratory (Russell-Hunter and Eversole, 1976, *Comp. Biochem. Physiol.* 54A:447; Russell-Hunter *et al.*,1983 *Comp. Biochem. Physiol.* 74A:491; Russell-Hunter *et al.*, 1984, *Ecology* 65:223). In both field and laboratory settings, there is good evidence for a tissue "degrowth" capacity in individual snails during overwintering conditions. Degrowth has been defined by Russell-Hunter and his colleagues as a decrease in unit mass of structural protein. When specimens of *Helisoma trivolvis* were held in a laboratory regime similar to winter conditions (8^0 C, no food), snails lost tissue biomass, including structural protein. Tissue degrowth was found in three of the four field populations studied by Russell-Hunter and his co-workers. The oxygen uptake and ammonia excretion rates also have been measured for individuals of *H.trivolvis* kept in laboratory degrowth conditions. These earlier studies provide some indication of the changing proportions of protein carbon and nonprotein carbon which are utilized as substrates in the degrowth physiology of *Helisoma trivolvis.*

Our work complements earlier studies by providing an age-specific experimental design and by including a related species, *Helisoma anceps* . We sampled a *H. trivolvis* population located in the Dawes Arboretum, near Newark, Ohio. Specimens of *H. anceps* were taken from a small spring-fed pond near Gambier, Ohio. Animals were collected in November, 1983, sorted by size and age, and maintained under simulated overwintering conditions in an environmental chamber set at 10°C, with a 14:10 light to dark cycle. Three hundred snails of each species were collected. The experimental design had three major categories of snails. One category was a pre-winter control group that was sacrificed shortly after collection. The other two categories were experimentals, snails that spent time in the laboratory under degrowth conditions. One of these categories was a fed group (offered an artificial food ration designed by Tashiro *et al.*, 1980, Malacol. Rev. 13:87), while snails in the other category were maintained without food. The "fed' and "unfed" groups were further divided into 35-day and 70-day subgroups, this designation representing the amount of time elapsing from the sacrifice of the controls to the sacrifice of a particular experimental subgroup. Finally, each experimental subgroup had old and young snails. The *H. trivolvis* population had one-, two-, and three-year-old animals (based on shell growth lines and size-frequency analysis). The *H. anceps* population had one- and two-year olds. We studied two- and three-year-old specimens of *H. trivolvis* and one- and two-year-old specimens of *H. anceps* . For each individual snail in all control and experimental groups and subgroups, we obtained oxygen consumptions, ammonia excretion, and urea excretion rates. These physiological measurements were made just prior to sacrifice of the animals. We also measured shell length, weighed shell $CaC0_3$, and determined shell-free tissue dry weights. There were no mortalities among the experimental animals.

There was evidence for degrowth in both species, regardless of whether or not food was available. The temperature regime of 10°C may be borderline for feeding activity. From our analysis of respiration rates in specimens of *H. trivolvis,* we conclude that rates in older animals (3-year-olds) decrease over a 70 day period of degrowth, while rates in younger animals (2-year-olds) increase. For *H. anceps,* respiratory rates of older snails (2-year-olds) increase during the degrowth period, but the rates of younger animals (1-year-olds) remained relatively constant during the degrowth regime.

The ammonia excretion patterns of *H. trivolvis* individuals were similar, regardless of age and trophic status. Rates were lower at 35 days, relative to both control values and rates measured at 70 days. In *H. anceps* individuals, there were age-specific and trophic-specific patterns of ammonia excretion. Younger fed animals had higher rates than older animals at the beginning of the experiment (controls) and at the 70-day sacrifice. The general patterns were a gradual increase in excretion rate through time for older animals, but a decrease (0 to 35 days) and then an increase (35 to 70 days) for young animals. In unfed specimens of *H. anceps,* young snails had higher rates of ammonia excretion at the beginning of the experiment and at the 35-day sacrifice.

The patterns of urea excretion were similar in unfed and fed, old and young specimens of *H. trivolvis.* There was a gradual increase in rates of urea excretion over the course of the 70 days of degrowth. For *H. anceps* individuals, urea excretion peaked at the 35-day sacrifice in both fed and unfed groups, but there was no clear age-specificity. Rates of unfed animals were greater than those fed during the experiment.

We conclude that there are clear species-specific and age-specific differences in the degrowth physiologies of *H. anceps* and *H. trivolvis.* Total nitrogen excreted (NH_3-N plus Urea-N) was fairly constant in specimens of *H. trivolvis.* For example, older unfed animals excreted roughly 7 to 10 ng $N \cdot hr^{-1}$ during the course of the experiment, but the proportion of urea excreted increased steadily from negligible amounts to greater than 60% of the total nitrogen excreted. In older unfed individuals of *H. anceps,* nitrogen excretion was highest in the 35-day sacrifices. In this species, total nitrogen excretion in older unfed animals ranged from roughly 20 ng $N \cdot hr^{-1}$ in controls, to almost 100 ng $N \cdot hr^{-1}$ in 35-day sacrifices, and back to about 45 ng $N \cdot hr^{-1}$ in the 70-day sacrifices. The proportion of nitrogen excreted as urea by older unfed *H. anceps* ranged from 80 to 95 percent and was highest in the 35-day sacrifices.

These preliminary studies provide important evidence for species- and age-specific physiological profiles in two *Helisoma* species. Importantly, and while there is considerable variation between species, our results are consonant with the paradigm that relative to older conspecifics younger snails have higher rates of protein turnover during diapause. Such turnover, whether it be for maintenance repair or for metabolic energy, may shape the age of first reproduction in temperate mollusk species which have an overwintering diapause state.

SOME PHYSICAL ASPECTS OF NAIAD DISTRIBUTION IN MISSOURI.

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The number of species and living specimens of naiades per site was correlated with physiographic region, stream order and gradient, and local soil type, bedrock type, and relief at 598 sites in Missouri. Both number of species per site and number of specimens per site were significantly positively correlated with stream order, and significantly negatively correlated with stream gradient. Neither number of species per site nor number of specimens per site was significantly correlated with physiographic region, or local soil or bedrock type, or local relief. The highest diversity and abundance of naiades occurs in the Missouri Ozarks where limestone and dolomite comprise a significant portion of the bedrock. The lowest diversity and abundance of naiades occurs in western and northern Missouri in areas of highly erosive soils.

DEVELOPMENT OF A HATCHERY FOR COMMERCIALLY IMPORTANT MARINE BIVALVES IN PANAMA.

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Scientists at the University of Delaware and the University of Panama are working together to establish an experimental hatchery for the production of juvenile clams *Protothaca asperimma,* scallops *Aequipectin circularis* and oysters *Pinctada mazatlantica, Ostrea irridescens.* The goal of the hatchery is to produce juvenile bivalves to replenish declining natural populations and to foster the development of bivalve aquaculture among coastal fishing families.

Reproductive cycles of commercially important bivalves in the Bay of Panama are poorly understood and appear to be significantly influenced by coastal upwelling which occurs during the dry season (January-April). Recent results of bivalve spawning trials, histological studies of gonadal development, and assessment of phytoplankton productivity in both natural waters and laboratory cultures are presented.

POPULATION BIOLOGY OF THE PLEUROCERID SNAIL, *LEPTOXIS CARINATA* (BRUG.) IN MARSH CREEK, ADAMS COUNTY, PA.

Sherman S. Hendrix, Biology Department, Gettysburg College, Gettysburg, Pennsylvania.

Both living and dead *Leptoxis carinata* (Brug.) were collected monthly from April 1969 to August 1970 using a modified Suber sampler in a tributary of the Potomac River, Marsh Creek, at highway US-30 four miles west of Gettysburg. Each monthly collection consisted of 30 samples of $.05m^2$ and included at least one transect across the stream above, within, and below a small riffle. Water depth, velocity, and bottom type were determined for each sample site. Marsh Creek is a typical piedmont bicarbonate stream with calcium ion ranging from 30-68 ppm, pH 7.3, and a cobble bottom predominating in the sampling habitat.

A total of 4684 live and 3225 dead *L. carinata* were recovered. The population exhibited characteristics similar to that reported by Aldridge (1982). Egg laying commenced in late March, peaked in June, and ceased by early August. Laboratory reared eggs hatched in 15 days at 20-22°C and young snails grew to a mean length of .639 mm in one week. Field collected young attained a length of 4.5 mm by the September collection and exhibited a high mortality rate. *L. carinata* became sexually dimorphic by the following summer. The sex ratio in the population was 1:1.

The digenetic trematode *Plagioporus hypentelii* Hendrix (1973) uses *L. carinata* as its first intermediate host. One and two year old males were found to have a significantly higher incidence of infection (7% vs 3%) than females. Infected individuals were usually found below the riffle. The number of daughter sporocysts in the rectum of *L. carinata* varied seasonally, with the peak in the summer months.

THE FRESHWATER MOLLUSKS OF THE HUDSON RIVER BASIN: A HISTORICAL AND ECOLOGICAL SURVEY.

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Except for Smith's recent papers (e.g., *Nautilus* 97: 128-131), the mollusk fauna of the Hudson River basin has received little attention. I am using museum and literature records in conjunction with field surveys to describe the distribution, ecology, and historical changes in status of the freshwater mollusks of the basin.

My survey of museum and literature records is nearly complete. Because of the dedication of a few collectors and the vigilance of several museums (ANSP, UMMZ, USNM, AMNH, MCZ), I was able to locate more than 2000 museum lots, most of them from the 19th century.

The Hudson basin's fauna contains at least 82 species of freshwater mollusks, including 21 unionids, 18 pisidiids, 24 pulmonates, and 19 prosobranchs. As Smith has already pointed out, the Hudson served as a zoogeographic gateway between the Atlantic Slope and the Interior Basin, so its fauna contains species from both of these zoogeographic regions. Of the 82 species in the fauna of the Hudson basin, 13 belong to the Atlantic Slope fauna, 17 belong to the Interior Basin fauna, and 52 species are widespread in both regions.

All distributional records from the museums, published papers, and this summer's survey of about 100 sites in the mid-Hudson valley are being put into a computer database and will be freely available to all scientists.

THE INFLUENCE OF SNAIL DENSITY AND SURFACE AREA ON THE GROWTH AND DEVELOPMENT OF *BIOMPHALARIA GLABRATA*.

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The prevention of the mollusc vectored parasitic disease schistosomiasis is of medical and social significance in many Third World countries. This parasitic disease results from infection by a cercarial population of the digentic trematode, *Schistosoma spp.*. *Biomphalaria glabrata* (Say) primarily a neotropical, hermaphroditic pulmonate (Gastropoda: Planorbidae) acts as an intermediate vector to *S. mansoni* principally in the Antilles archipelago and certain South American countries.

The increased incidence of infection in these developing countries, in part, is due to increased population growth, limited water resources and agricultural technology. Techniques for the control of schistosomiasis have incorporated molluscicides, chemotherapy, habitat alteration and biological control. These methods have facilitated a containment of the disease in limited locations but not its eradication.

In order to improve strategies for control of the vector, this laboratory study was designed to explore the influence of substratum availability and population density on the life history of *B. glabrata*. Four initial cohort populations of 5, 10, 25 and 50 sexually immature snails were examined in five surface area modifications for a 25 week period. Augmentation of the surface area over that provided in the control aquaria was furnished through the addition of vertically suspended artifical aquarium plants. The factorial design allowed for the weekly examination of the parameters of individual growth rates, reproductive rates and population growth. The environmental conditions of water volume, depth, light, and temperature were controlled. Food was supplied in excess of requirements and a recirulating water supply system was designed to negate interferrence from hypothesized snail and/or plant derived metabolites.

Average growth curves for individuals of each of the twenty populations, plotted as the average shell diameter versus snail age, displayed asymptotic growth. The maximum average shell diameter was calculated using the Fort-Walford plotting method. These values ranged from 15.2 to 26.4 mm, with no discernable trend between the size and either variable. The rate of growth was evaluated following linearization of the growth curve. Regression analysis of the rate of growth and the dependent variables, snail density and surface area, yielded a statistically insignificant F value ($P = .05$).

Ovipositing commenced when the snails reached 9 mm shell diameter. The existance of a linear relationship was confirmed between the total number of egg masses and the number of reproductive snails for each population. The slope values from these plots were utilized to assess the influence of augmented surface area on reproductive rates. A regression analysis produced a statistically insignificant F value ($P = .05$).

Population growth was monitored by simultaneously plotting initial cohort survival and total population number over time. Following an initial period of population stability, representing sexually immature snails, each population entered a phase of logarithmic growth. This expanse was followed by a sudden decline in numbers. Depending on the intensity and duration of the growth phase, the populations tended towards equilibrium by exhibiting either a precipitous drop and incremental fluctuations, or a cyclic trend of damped oscillations prior to equilibration. The fluctuations in the numbers of snails and ultimate convergence upon a stabilized population can best be explained by changes in the survival rates of offspring. The intrinsic rate of natural increase 'r', for each population was calculated using an iterative solution. When examined in a multiple regression model, a statistically insignificant F value was obtained for the variable, surface area; however, a significant F value ($P = .05$) was yielded for snail density.

It is apparent that over the ranges examined, neither surface area augmentation nor snail density influenced the rate of morphometric growth or reproduction. Population growth appears to be influenced by snail density. This suggests that at high densities, populations are not regulated by reduced fecundity, but through increased juvenile mortality. To optimize molluscicliding techniques it may be incumbent upon researchers to examine not only climatic events regulating population levels, but intrinsic control mechanisms as well.

GROWTH LINES IN ACETATE PEELS OF THE CHONDROPHORES OF *MYA ARENARIA* AND *M. TRUNCATA*.

John W. Ropes and **Maurice K. Crawford.** National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole Laboratory, Massachusetts.

The soft-shell clam, *Mya arenaria*, has been a traditional source of clam meats in New England since colonial days. Landings in 1984 were 7.9 million pounds of meats worth $19,842,000 to the fishermen. In past investigations of the clam's life history, age was determined from external valve rings. This often produced unsatisfactory results because of the poor definition of the rings formed in the valves of this deep burrowing benthic bivalve.

Recent investigators have reported finding useful internal age/growth lines in 35-40 μm-thick sections of the chondrophore in the left valve of soft-shell clams. In general, the fragile nature of the shell makes routine production of such thin sections technically difficult.

An alternate method was developed, based on a technique of preparing acetate peels of ocean quahog, *Arctica islandica*, valves for age determination. Internal age/growth structures in the chondrophores of *M. arenaria* and the truncate soft-shell clam, *M. truncata*, were revealed by radially sectioning valves embedding them in an epoxy resin, polishing the cut edges to a high luster and then etching the cut edges with 1% HCl for 1 minute before applying sheet acetate with acetone. After a drying period, the acetate was peeled off and sandwiched between glass slides for microscopic examination.

Successive growth lines clearly separated growth increments and were suggestive of a definite change in microstructural elements in the chondrophores of both *Mya* species. The boundaries of growth increments were more clearly defined by the growth lines in the peels than in thin-sectioned preparations. Research is in progress to accumulate evidence validating the suspected annual periodicity of the growth lines.

WHY "START" LATE: THE AGE OF FIRST REPRODUCTION IN *MELAMPUS BIDENTATUS*. Jay Balboni-Tashiro, Amy Bowser, George Cohen, Liz Sigel, and **Patricia Walborn,** Kenyon College, Gambier, Ohio.

Specimens of *Melampus bidentatus* from the Little Sippewisset Marsh (Falmouth, MA, U.S.A.) have been experimental subjects in a broad range of physiological, ecological, and biochemical studies. The Little Sippewisset Marsh population of *Melampus* has been studied by Russell-Hunter and his colleagues for almost two decades. Following elegant studies of the life cycle and life-history (Apley, 1970, *Malacologia* 10:381; Russell-Hunter *et al.*, 1972, *Biol. Bull.*143:623), several other investigations have used specimens of *Melampus* from the Little Sippewisset population. These studies include measurements of respiratory rates (McMahon and Russell-Hunter, 1981, *Biol. Bull.* 161:246), neurosecretion (Price, 1979, *J. Exp. Zoo.* 202:269), water relations (Price, 1980, *J. Exp. Mar. Biol. Ecol.* 45:51), and tidal migrations (Price, 1984, *J. Exp. Mar. Biol. Ecol.* 78:111). Most recently, we have examined the overwintering diapause state in specimens of *Melampus* from the Little Sippewisset Marsh and from a population near Weymouth, Massachusetts (Tashiro *et al.*, 1983, *Biol. Bull.* 165:511). Preliminary age-specific bioenergetic partitioning studies have also been completed, as well as a survey of age-specific gonad changes during the final breeding cycle in the summer of 1983 (Tashiro *et al.*, 1984, *Biol. Bull.* 167:515).

Melampus bidentatus is an ellobiid species found in the high littoral zones of semi-enlosed salt marshes along the North American Atlantic coast from New Brunswick (Canada) to Texas (U.S.A.). This species is amphibious, but has a planktonic veliger larva. There is close coupling between spring tide submergence of the *Melampus* habitat and copulation, oviposition, and hatching. Individuals of this species can exist as largely terrestrial animals because of the semilunar synchrony in their reproductive cycles. The studies mentioned above provide evidence of other behavioral and physiological adaptations that potentiate an amphibious existence. In the Little Sippewisset Marsh, individuals of *Melampus* have a life-span of three to four years. The species *Melampus bidentatus* is a simultaneous hermaphrodite, an iteroparous breeder, and previous studies have reported three to four breeding cycles during the summer. The same studies reported that two- and three-year-olds contributed to the reproductive effort during the summer breeding cycles.

For several months each year, whenever the temperature falls below 13°C, individuals enter a diapause state. We feel that diapause imposes physiological constraints on the age of first reproduction. There is protein degrowth in overwintering specimens of *Melampus*, but this degrowth is age-specific, younger animals losing proportionately more protein than older snails. Such protein degrowth is most likely maintenance repair, younger snails having more efficient repair systems that break down tissue protein in order to reutilize amino acids. Rates of protein sythesis appear to be faster in diapausing younger snails (Tashiro, unpublished) and this corroborative evidence bolsters our contention that younger snails have higher rates of maintenance repair. Rates of emergency repair were measured in diapausing snails that had one tentacle ablated (Tashiro, *et al.*, 1983, *Biol. Bull.* 165:511). Again, there was age-specificity, younger animals having higher rates of tentacle regeneration than older animals.

We hypothesize that overwintering repair delays the age of first reproduction in *Melampus bidentatus*. Previous studies had reported reproduction in two- and three-year-olds, with a minimum size for reproduction being about 5.8 mm. However, no age-specific quantification of reproductive effort has been reported for the first breeding cycle of a summer. Degrowth could impose a physiological debit that might not be reconciled by the time of the first breeding cycle. Since degrowth is proportionately greater in younger animals, only three-year-olds might lay eggs during the first breeding of a summer.

We have begun to test our hypothesis by collecting data on gonad changes (dry weight, carbon, protein), age-specific fecundity, and by experimental manipulation of degrowth conditions in the laboratory. Earlier preliminary work on changes in gonad protein during the final breeding cycle of 1983 showed that both two- and three-year-olds lose gonad protein, but two-year-olds have a slower rate of loss. We now have compared gonad and tissue dry weights in post-winter and pre-breeding snails collected in 1985. Post-winter (March) two-year-olds have a gonad to somatic weight ratio of .04, while three-year-olds have a ratio of .06. By the time of the first breeding cycle (late May), the gonad to somatic ratios of two- and three-year-olds were not significantly different. We used a ratio of gonad dry weight to shell length as a crude size-specific index for gonad condition in two- and three-year old specimens of *Melampus*. During the first breeding cycle of 1985, three-year-olds laid eggs and there was a decline in the gonad weight to shell length ratio for this age group. Two-year-olds did not lay eggs during the first breeding cycle and their gonad weight to shell length ratio increased during the first breeding period. Interestingly, during the second breeding cycle in 1985, younger snails appeared to have a smaller reproductive effort in terms of average number of eggs laid.

We feel these preliminary data are partial support for the hypothesis that degrowth is one of the causal agents delimiting the age of first reproduction in specimens of *Melam-*

pus bidentatus. Of course, we need to complete long-term analyses of gonad changes and to refine experimental manipulation of degrowth conditions in laboratory setting (e.g. the effects of different temperature regimes). We do know that during the first breeding cycle of 1985, two-year-olds did not contribute to the reproductive effort. Furthermore, the minimum size for reproduction is not 5.8 mm for two-year-olds in the first breeding periods. Our work is continuing this summer and through the next year.

HOST SPECIFICITY OF AN ECTOPARASITIC SNAIL IN THE GENUS *ODOSTOMIA* IN THE PANAMA BAY REGION (GASTROPODA: PYRAMIDELLIDAE). J.E. Ward. University of Delaware, College of Marine Studies, Lewes.

Many species of snails in the family Pyramidellidae are ectoparasitic on other marine invertebrates. Varying degrees of host specificity have been reported for many North American and European pyramidellids. However, host preferences of tropical parasitic pyramidellids are not known, and little has been reported on their feeding behavior or ecology.

In this study, ectoparasitic pyramidellids were collected in Panama Bay, Panama, from encrusting organisms. One abundant species was tentatively identified as belonging to the genus *Odostomia*, subgenus *Chrysallida*. Qualitative field and laboratory observations and quantitative choice experiments determined that this species of *Odostomia* feeds preferentially on serpulid polychaete worms. However, these ectoparasites are not host specific and can parasitize several species of bivalves common to the Panama Bay region.

ANNUAL BUSINESS MEETING
REPORT FOR 1985

The 51st annual meeting of the American Malacological Union convened at 2 p.m. in Chaffee Hall on the campus of the University of Rhode Island, Kingston, Rhode Island, with Dr. Melbourne Carriker, president, presiding.

Dr. Carriker announced that there were 192 registrants, with 15 from abroad.

The following Resolution from Council was adopted unanimously: "Whereas one of our present Honorary Life Members, Harald A. Rehder, is our oldest past President, an original charter member, and a lifelong, active supporter of the AMU with impeccable malacological qualifications, we the undersigned wish to join others and nominate Harald A. Rehder as our Honorary Life President."

Student awards for this meeting were accepted as follows: one $250.00 award in memory of Dr. William J. Clench, given by Constance E. Boone, and one $250.00 award in memory of Dr. Joseph Rosewater, given by Anne Joffe.

Dr. Robert Prezant, Editor, announced the recipients of these awards to be Janice Voltzow and Silvard P. Kool.

Dr. Clyde F. E. Roper spoke in memory of Dr. Rosewater, and Dr. Dorothea Franzen presented memorial remarks about Dr. Dee Dundee, both former presidents of AMU who died in 1985.

Minutes of the 1984 meeting as published in the *Bulletin* were approved. Summaries of officer and committee reports were approved, and full accounts are filed with the Recording Secretary.

Membership and subscriptions for 1984 totalled 782. Because the report on memberships included a statement remarking on the slowness of payment of dues, the following motion was approved:

"No member of AMU will receive the AMU *Bulletin* until dues are paid for the year in which the *Bulletin* volume in question is issued."

The financial report for fiscal year 1984, as approved by the audit committee and Council, and approved at the general meeting, is printed elsewhere in this Bulletin.

Dr. Prezant, Editor, reported plans for special editions of the *American Malacological Bulletin*, the first just off press and presented at this meeting. "Perspectives in Malacology," Special Edition 1, contains the symposium held in honor of Dr. Carriker on his retirement in the spring of 1985 from the University of Delaware at Lewes. The second Special Edition will be on *Corbicula* and is due late in 1985. The third will be on larval oysters. All such editions are underwritten completely, and AMU will benefit from sales.

On recommendation from the Editor, the following motion was approved: "The *American Malacological Bulletin* separate account, now under editorial control, will be transferred to the Treasurer to be maintained in a separate *Bulletin* account."

The following slate of officers due to be elected at this meeting was unanimously approved:

President:	James Nybakken (one year term)
President-elect:	William Lyons (one year term)
Vice-President:	Richard E. Petit (one year term)
Recording Secretary:	Constance E. Boone (three year term)
Councillor-at-large:	Mark Gordon (two year term)
Councillor-at-large:	Bowie Kotrla (two year term)

Richard E. Petit, Finance Committee chairman, enumerated efforts to increase membership which included writing letters to former members and to non-member malacologists who published last year. Letters of appreciation to donors of materials or cash had been written. This year's auction had raised $954.95. (With the addition of donations from members during the year totalling $413.50 and the gift of $1,000 from Dr. Louise Russert Kraemer at this meeting, the Symposium Endowment Fund now stands at $20,421.94.)

Mr. Petit explained a plan to reprint older unavailable malacological publications as a means of raising money. Report approved.

The AMU Budget voted for 1986:

INCOME	
MEMBERSHIPS (all except life)	$13,500.00
SALES	
Bulletin Supplements	3,000.00
HTSCS	300.00
Bulletin Back Issues	600.00
Teskey Index	25.00
Subtotal sales	(3,925.00)
BULLETIN receipts (Page charges, etc.)	3,300.00
Proceeds from the meeting	2,000.00
Donations, symposium of that year	500.00
Miscellaneous	50.00
Interest, Symposium Endowment Fund	2,000.00
Interest, General Savings and Life Membership Fund and Bulletin account	2,230.00
TOTAL	$27,505.00

DISBURSEMENTS

BULLETIN publication costs (Including supplements)	$39,000.00
Newsletter	1,200.00
Membership committee	100.00
President's Organizing Fund	600.00
Officers to meeting	3,200.00
California Filing Fee	12.50
Postage	1,200.00
Printing	300.00
Office Supplies	150.00
Miscellaneous (incl. telephone)	300.00
Annual meeting expenses	150.00
Advertisements	500.00
Archives equipment and supplies	250.00
Memberships (WSM, ASC, etc.)	60.00
Symposium expenses (Endowment Fund interest)	2,000.00
Student Prize, best paper at meeting	250.00
TOTAL	$49,322.50

SUMMARY

BULLETIN account balance as of Jan. 1, 1986	$28,500.00
Income	27,505.00
Disbursements	49,322.50
NET GAIN	6,682.50

The following change in the Constitution was approved, subject to mail vote by all members:

Article IV, Section 1

The government of the AMU shall be vested in an elected Council which shall consist of:

a. Currently elected officers,
b. The immediate past three (3) Presidents,
c. Two (2) Past Presidents whose terms as President ended 4-10 years prior to their election to this post, each serving two years with one elected each year but not serving consecutive terms, and
d. Two (2) Past Presidents whose terms as President ended more than 10 years prior to their election to this post, each serving two (2) years with one elected each year but not serving consecutive terms.

The following change in the By-Laws was voted:

Article IV, Section 2

The Nominating Committee shall consist of not more than five persons but must include one Councillor-at-Large, one immediate Past President, and one Past President whose term ended 4 or more years ago. They shall prepare a slate of candidates to fill any vacancy for the ensuing year ....

Dr. Nybakken discussed plans for the 1986 meeting to be held in Monterey, California, starting on Wednesday, July 1st and ending July 6th with a field trip to Moss Landing and possibly a dredging trip. WSM will join AMU for this meeting. The Monterey Peninsula Shell Club will assist the president.

There will be three symposia: one on the biology of the Opisthobranch Molluscs organized by Dr. Terry Gosliner and honoring Dr. Eveline Marcus on her 85th birthday, another on Molluscan Morphometric Analysis organized by Drs. Carole Hickman and David Lindberg, and a third on cephalopods planned by Dr. Roger Hanlon, with a display of Stillman Berry Memorabilia.

A choice of field trips will be offered to Asilomar for marine molluscs, to Capitola for fossils, and to the State of California Shellfish Laboratory at Granite Canyon on the Big Sur Coast. A special afternoon visit to the new Monterey Bay Aquarium on Cannery Row has been arranged, with Dr. Steve Webster, director of education, giving a short talk on the aquarium. Dr. Michael Ghiselin, the MacArthur Fellow, will be the banquet speaker.

All meetings will be held at the new Sheraton Hotel right in the heart of Monterey. Rooms will be $90.00 per room.

A motion was voted stating that the 1987 meeting would be held in Florida.

Alan C. Buchanan presented the Conservation Committee report, with the following points of importance:

1. Copies of the Federal Register review of invertebrate species proposed for listing as of May 22, 1984, were distributed. Any input from AMU members regarding these species should be sent to Jim Williams or Steve Chambers of the U.S. Fish and Wildlife Service.
2. The Tar River Spiny Mussel has been listed as endangered, and the James River Spiny Mussel has been proposed for listing. A number of species from the Tombigbee River has been proposed for listing.
3. Last year AMU sent a letter to the U.S. Fish and Wildlife Service requesting action to protect *Io fluvialis,* and this service has recently responeded that *Io* will be listed. This will protect a portion of the Clinch River.
4. The Nature Conservancy has a list of habitats (areas) which need special action and protection.

The report included a number of special conservation projects and research efforts by AMU members, to be included in the Newsletter.

The report approved from the Council of Systematic Malacologists included the following points: (Presented by Dr. Richard S. Houbrick, president).

1. Dr. Donna Turgeon presented a status report on the Common Names List, which includes 4700 species compiled by over 100 contributors and reviewers. The work will be published within the year, in hard and soft-bound editions, by the American Fisheries Society. Once AFS's publication costs have been recovered through sales, AMU will receive 50% of the profits. A five-year standing committee in CSM was established to oversee the project.
2. Dr. Houbrick reported on progress of the CSM

faunal survey of U.S. freshwater and terrestrial molluscs and announced that Dr. Barry Roth has agreed to coordinate efforts in the Western U.S.

3. Dr. Pratt was elected chairman of the newly proposed committee to provide a checklist of North American Mollusca, beginning with the non-marine molluscs of North America north of Mexico.
4. Dr. Alan Solem reported on the status of malacological curatorial positions worldwide, noting that there has been a drastic decrease in the U.S. He stressed the immediate need to improve the visual image of malacologists to make them more competitive in the current and future job markets. A committee to implement the existing "National Plan," with Dr. Solem as chairman, was approved.
5. A letter from the Council of Systematic Malacologists and the American Malacological Union was sent to the directors and trustees of the Bernice P. Bishop Museum strongly recommending that they reestablish the position of Terrestrial Malacologists so that the research activities of this museum could continue.
6. Dr. Donna Turgeon was elected by unanimous vote as President of CSM, to serve a three-year term.

A motion was approved directing the current President to establish a committee to recommend the most appropriate uses of the Maud Nickerson Meyer legacy to AMU. Dr. Carriker appointed Drs. Robert Robertson and Louise Kraemer and Anne Joffe to this committee.

A motion was approved making the student paper award for 1986 $500.00, with the acceptance of a gift of $250.00 from Constance E. Boone to be added to the AMU budgeted amount.

A motion was approved making the goal for the Symposium Endowment Fund $30,000.

Dr. Turgeon rose to express appreciation to Dr. Carriker for this successful meeting and presented him with a pastel portrait she had done from a photograph.

Meeting adjourned at 3:30 p.m.

Constance E. Boone, Recording Secretary

FINANCIAL REPORT

REPORT OF THE TREASURER FOR THE FISCAL YEAR ENDING DECEMBER 31, 1984

CHECK BOOK BALANCE, JANUARY 1, 1984			$ 2,635.69
RECEIPTS:			
Memberships:			
Regular	$ 8,465.00		
Life	100.00		
Sustaining	181.50		
Student (regular)	422.00		
Student (foreign)	36.00		
Corresponding	602.50		
Clubs	773.00		
Institutions	3,043.00		
	13,623.00	13,623.00	
Sales:			
AMU BULLETIN Back Issues	616.50		
Teskey Index	19.00		
Rare & Endangered Species	6.25		
HOW TO STUDY AND COLLECT SHELLS	321.14		
	962.89	962.89	
Other Receipts:			
Best Student Paper Donations	100.00		
Endowment Fund Donations	1,882.50		
1984 Auction Proceeds	2,232.25		
Proceeds from Norfolk Meeting	5,341.51		
Endowment Fund Interest Withdrawn	1,648.13		
Interest on Life Membership	763.65		
Memorials	20.00		
Refund on Air fare for Myra Taylor	24.50		
Payment for Fossil Book	21.00		
Check Re-deposit	20.00		
Miscellaneous donations	23.50		
	12,077.04	12,077.04	
Total Cash Receipts Accounted For	26,662.93		26,662.93
TOTAL CASH ACCOUNTED FOR			$ 29,298.62

DISBURSEMENTS:

AMU BULLETIN, incl. postage, printing, etc.	$ 9,046.78	
AMU NEWSLETTER, incl. postage, printing, etc.	1,482.55	
Other Postage	1,120.58	
Other Printing	278.03	
Office Supplies	154.11	
Dues and Advertising	382.00	
AMU-Norfolk Tee Shirts	567.52	
Officers' Travel - Norfolk	1,789.68	
Membership Brochures	115.62	
Symposium Endowment Fund Deposits (includes $500.00 from AMU-Budget item)	5,817.59	
Symposium Expenses - Norfolk	1,500.00	
Student Awards	500.00	
Payment for book (fossil)	21.00	
Bank charges, incl. Returned check for signature	43.49	
Miscellaneous, incl. Phone Calls	96.63	
TOTAL DISBURSEMENTS FROM ALL ACTIVITIES		22,915.58
CHECK BOOK BALANCE, JANUARY 1, 1984		2,635.69
TOTAL RECEIPTS		26,662.93
TOTAL CASH		29,298.62
TOTAL DISBURSEMENTS		22,915.58
CHECK BOOK BALANCE, DECEMBER 31, 1984		6,383.04

RECAPITULATION OF ASSETS, DECEMBER 31, 1984:

Cash in Checking Account, Mercantile Bank	$ 6,383.04
Treasurer's Petty Cash	20.00
Recording Secretary's Petty Cash	300.00
Corresponding Secretary's Petty Cash	75.00
Editor's Fund	6,322.14
SASA Acct. #22-906859	3,282.64
First Federal Acct. #6300834-02	5,262.43
First Federal Acct. #6800057-02	2,684.22
Bexar Savings Acct. #501-900-03	11,437.74
Life Membership Account #22-906859	3,193.78
TOTAL ASSETS	$38,960.99
AMU NET WORTH, DECEMBER 31, 1984	38,960.99
CHANGES IN CAPITAL ACCOUNT:	
AMU Capital Acct., January 1, 1984 (Incl. Life Membership)	$24,357.95
AMU Capital Acct., December 31, 1984	20,832.70
NET INCREASE IN ASSETS, 1984	14,603.04

Respectfully submitted,
MYRA L. TAYLOR, Treasurer 1984

AMERICAN MALACOLOGICAL UNION, INC.
EXECUTIVE COUNCIL
1985-1986

OFFICERS

President	James Nybakken
President Elect	William G. Lyons
Vice-President	Richard E. Petit
Treasurer	Anne Joffe
Recording Secretary	Constance E. Boone
Corresponding Secretary (Newsletter Editor)	Paula Mikkelsen
Bulletin Editor	Robert S. Prezant
Councillors-At-Large	Roger Hanlon, John B. Burch Mark Gordon, M. Bowie Kotrla

COUNCIL
PAST PRESIDENTS
(Current Members)

Harald A. Rehder (1941)
Henry van der Schalie (1946-47)
A. Myra Keen (1948)
Ruth D. Turner (1957)
R. Tucker Abbott (1959)
Thomas E. Pulley (1961)
William K. Emerson (1962)
Albert R. Mead (1963)
Juan J. Parodiz (1965)
Ralph W. Dexter (1966)
Arthur H. Clarke (1968)
Alan Solem (1970)
David H. Stansbery (1971)
Arthur S. Merrill (1972)
Harold D. Murray (1974)
Donald R. Moore (1975)
Dorothea S. Franzen (1976)
George M. Davis (1977)
Carol B. Stein (1978)
Clyde F. E. Roper (1980)
Richard B. Houbrick (1981)
Louise Russert-Kraemer (1982)
Alan J. Kohn (1983)
Robert Robertson (1984)
Melbourne R. Carriker (1985)

HONORARY LIFE PRESIDENT

Harald A. Rehder

HONORARY LIFE MEMBERS

R. Tucker Abbott
A. Myra Keen
Harald A. Rehder
Margaret C. Teskey
Ruth D. Turner
Henry van der Schalie

THE AMERICAN MALACOLOGICAL UNION MEMBERSHIP

(Revised October 15, 1985)

ABBOTT, DR. R. TUCKER, P. O. Box 2255, Melbourne, FL 32901.

ADAMKEWICZ, DR. S. LAURA, Dept. of Biology, George Mason University, Fairfax, VA 22030 (Genetics, particularly the population genetics of marine bivalves).

AHLSTEDT, STEVEN, 11 E. Norris Rd., Norris, TN 37828 (Biological aide in Fisheries Management, TVA).

ALDRIDGE, DAVID W., Dept. of Biology, North Carolina A&T State University, Greensboro, NC 27411.

ALEXANDER, ROBERT C., 423 Warwick Rd., Wynnewood, PA 19096.

ALLEN, JAMES E., 1108 Southhampton Dr., Alexandria, LA 71301 (Tertiary micro-mollusca).

ANDERS, MS. ALICE D., 749 Cardium St., Sanibel, FL 33957 (Fossils, live marine studies).

ANDERS, KIRK W. SHELLS OF THE SEAS, INC., PETE BRIGHT, vice-president; P. O. Box 1418, Ft. Lauderdale, FL 33302 (Buy, sell, trade specimen shells; shelling tours worldwide).

ANDERSON, CARLETON JAY JR., 56 Kettle Creek Rd., Weston, CT 06883.

ANDERSON, ROLAND C., The Seattle Aquarium, Pier 59, Waterfront Park, Seattle, WA 98101 (Invertebrate husbandry and natural history).

ANDREWS, DR. JEAN, 2710 Hillview Green Lane, Austin, TX 78703.

ARDEN, GEORGE J. JR., 122 E. 38th St., New York, NY 10016 (Cowries; effects of pollution on marine life in general).

ARMINGTON, STEWART F. AND LEE, 15932 Brewster Rd., Cleveland, OH 44112 (Shells with postage stamps and worldwide marine).

AROCHA, LICENIADO (LIC., MSC) FREDDY, Apartado #204, Cumana-6101, Venezuela (Biology and fisheries of cephalopods).

ASHBAUGH, KAREN, 9045 Comet St., El Paso, TX 79904.

ASHWELL, JAMES R., 2125 Mohawk Trail, Maitland, FL 32751 (General).

ATHEARN, HERBERT D., Museum of Fluviatile Mollusks, Rt. 5, Box 499, Cleveland, TN 37311 (Freshwater mollusks).

ATKINSON, DR. JAMES W. AND ELIZABETH H., Dept. of Natural Science, Michigan State University, East Lansing, MI 48824 (Developmental biology; Terrestrial pulmonates—special emphasis on pattern formation in relation to spiral cleavage and gametogenesis—also evolutionary mechanisms which emerge from developmental events).

AUFFENBERG, KURT, Museum Technician, Florida State University, Univ. of Florida, Museum Road, Gainesville, FL 32611 (Neritacea: Neritidae).

AVELLANET, MRS. HELENE, 105 Clipper Way, Fair Winds Villas, Nokomis, FL 33555.

AVILES E., PROF. MIGUEL C., Apartado 6-765, Zona Postal El Dorado, Panama, Rep. of Panama (Histology and embryology).

BABRAKZAI, DR. NOORULLAH, Dept. of Biology, Central Missouri State Univ., Warrensburg, MO 64093.

BAERREIS, DAVID A., Box 4651-406 Beimer Ave., Taos, NM 87571 (Paleoecological interpretation through mollusks).

BAILEY, JUNE E., 813 Bayport Way, Longboat Key, FL 33548.

BAKER, MRS. HORACE B., 11 Chelton Rd., Havertown, PA 19083.

BAKER, JOHN A., 147 Hedgegrove Ave., Satellite Beach, FL 32937 (Study and collection of marine Bivalvia and land and tree snails).

BALBONI-TASHIRO, DR. JAY SHIRO, Dept. of Biology, Kenyon College, Gambier, OH 43022 (Physiological ecology of fresh waters: molluscan fauna; salt-marsh ecosystems: molluscan fauna).

BANKSTON, DR. CECIL N. JR., 4841 Woodlake Dr., Baton Rouge, LA 70816 (Marine shells).

BARBER, DR. BRUCE J., Rutgers Shellfish Laboratory, P. O. Box 587, Port Norris, NJ 08349 (Physiology, reproduction, and parasitology of marine bivalves).

BARGAR, TOM AND DENISE SCHNEIDER-BARGAR, 1235 N. 7th St., Lincoln, NE 68508 (Functional morphology of gastropods).

BARLOW, MRS. G. BARTON (ALICE), 76 Westervelt Ave., Tenafly, NJ 07670.

BATEMAN, JAMES R., P. O. Box 2036, Neptune City, NJ 07753-2036 (New Jersey shells, intertidal to 100 fms.; also systematics of *Strombus* and *Cymatium,* worldwide distribution and variation).

BAUER, LAURA M., Apt. 346, 2228 Seawall Blvd., Galveston, Texas 77550.

BAXTER, RAE, Box 96, Bethel, AK 99559-0096 (Area of interest: Alaska and the Arctic; all species of mollusks, land, freshwater, and marine; microshells).

BAYLISS, RICHARD R. AND MARLENE, 1557 Argonne Road, Reading, PA 19601 (Florida and Caribbean shells).

BAZATA, KENNETH R., 5440 Cleveland, Apt. 9, Lincoln, NE 68504 (Terrestrial pulmonates; *Dentalium*).

BEETLE, MS. DOROTHY E., 407 Thunderbird Drive, Fort Collins, CO 80525.

BELANGER, SCOTT E., Univ. Center for Environmental Studies, Virginia Polytechnic Institute and State Univ., Blacksburg, VA 24061 (*Corbicula* ecology, industrial biofouling by *Corbicula*, aquatic ecotoricology).

BERMUDEZ, ALEJANDRO, P. O. Box 68, Missouri City, TX 77459 (*Murex* and nudibranchs of the Caribbean area).

BERRY, DR. ELMER G., 8506 Beech Tree Court, Bethesda, MD 20817.

BERSCHAUER, DAVID P., Dept. of Ecology and Evolutionary Biology, Univ. of California, Irvine, CA 92715 (Gastropods, esp. *Tegula*, abalone, *Calliostoma*; competition and predation).

BILLUPS, DR. CHARLES W., 2021 Firetower Lane, Ijamsville, MD 21754 (Power plant cooling systems effects, biofouling of cooling water systems, *Corbicula,* endangered mussel species).

BIPPUS, EMMA LEAH, 2743 Sagamore Rd., Toledo, OH 43606 (Marine gastropods).

BISHOF, DAVID, 994 68th St. Ocean, Marathon, FL 33050.

BLAIR, LUCIANNE, 1033 Rockcreek Drive, Port Charlotte, FL 33948.

BLEAKNEY, DR. J. SHERMAN, Dept. of Biology, Acadia Univ., Wolfville, Nova Scotia, Canada BOP 1XO (Nudibranchs, sacoglossans; ecology, zoogeography, systematics).

BLEDSOE, WILLIAM D., 352 Bon Hill Rd., Los Angeles, CA 90049.

BLOOM, JONATHAN A., RR6, Box 122, Town and Country TR CT., Carbondale, IL 62901 (Temporal changes in species diversity of freshwater mussels in Eastern U.S.).

BLUM, BERNARD J., 67-11 Beach Channel Drive, Arverne, Queens, NY 11692 (*Donax*).

BODY, RALPH L., 2538 10th Ave. W., Seattle, WA 98119 (Taxonomy).

BOGAN, ARTHUR E., Dept. of Malacology, ANSP, 19th and the Parkway, Philadelphia, PA 19103.

BOGG, JEAN A., #301, 3055 N. Riviera Drive, Naples, FL 33940.

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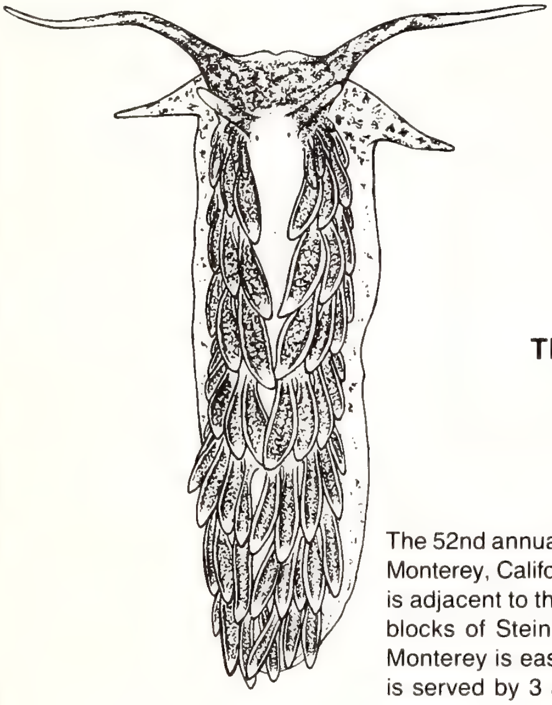

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MONTEREY, CALIFORNIA
THE SHERATON HOTEL
JULY 1-6, 1986

The 52nd annual meeting of the American Malacological Union will be held in historic Monterey, California from July 1-6, 1986 at the new Sheraton Hotel. The new Sheraton is adjacent to the famous Fisherman's Wharf with its many restaurants, within a few blocks of Steinbeck's Cannery Row, and is surrounded by many historical sites. Monterey is easily accessible by air from either Los Angeles or San Francisco and is served by 3 airlines.

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Beattie, J. H., K. K. Chew, and W. K. Hershberger. 1980. Differential survival of selected strains of Pacific oysters (*Crassostrea gigas*) during summer mortality. *Proceedings of the National Shellfisheries Association* 70(2):184–189.

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Cover. Egg capsules of some small marine prosobranchs. For full details see paper in this volume by D'Asaro, pages 185-199.

THE AMERICAN MALACOLOGICAL BULLETIN (formerly the Bulletin of the American Malacological Union) is the official journal publication of the American Malacological Union.

AMER. MALAC. BULL. 4(2)
August 1986

VARIABILITY IN GROWTH OF HARD CLAMS, *MERCENARIA MERCENARIA*[1]

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ABSTRACT

Growth and survival of hard clams, *Mercenaria mercenaria* (L.), were determined for 13-month old individuals grown for 4.5 years in protected trays in a subtidal site in South Carolina. Calculated annual mortality rate was 4%. Most growth (change in shell length, SL) occurred in the first 2 years. Growth appeared to be a function of age and size with younger clams of the same size growing faster than older clams. Similarly, smaller clams grew faster than larger clams of the same age. The smaller clams were consistently faster growers through a size of 60 mm SL and an age of 53 months. Growth rates of individual clams varied widely between time intervals. Correlation coefficient computed between initial SL (at planting) and growth was negative (-0.44) suggesting that smaller clams exhibited compensatory growth. These results are discussed in relation to the mechanisms of growth in clams and the development of protocols for selecting fast growing clams for culture.

The growth characteristics of hard clams, *Mercenaria mercenaria* (L.), throughout its geographical range have been determined (Ansell, 1968); however, very little information is available for South Carolina, Georgia and the east coast of Florida. In the early 1970's several investigations were initiated to provide information on growth of hard clams along the South Carolina coast (e.g. Eldridge *et al*., 1976, 1979). Through a routine sampling program to determine the effects of increased population density on survival and growth of hard clams, considerable variation in size (growth) was observed. Variations in growth were not only observed under different environmental conditions (e.g. population density levels), but also among clams of the same age growing under apparently uniform conditions. In view of these observations, individual clams of known age were marked in order to monitor individual growth. A second objective of the study was to obtain an estimate of mortality without predation.

MATERIALS AND METHODS

In May 1975, hatchery seed clams approximately 5 months old and 13 mm in shell length, obtained from Coastal Zone Resources Corporation of North Carolina, were planted and held in Clark Sound, South Carolina until January 1976. At that time, clams were large enough ($\bar{X}$ shell length = 24.7 mm) to be numbered with Testors' enamel paint on one shell valve and Sanford's Sharpie felt-tip pen on the other valve. A total of 313 clams were marked and measured for shell length (anterior-posterior axis, SL), shell height (dorso-ventral axis, SH) and shell width (lateral axis, SW) with vernier calipers to the nearest 0.1 mm (see Fig. 1).

Clams were planted in equal numbers (stocking density of approximately 226 clams/m^2) in 2 oyster trays (118 X 61 X 14 cm) filled with 14 cm of natural sediment. Trays were supplied with protective lids made of 5-mm mesh plastic cloth and placed in a subtidal site that was approximately 0.5 m below mean low water. This area is characterized by mostly sand (20-30% silt-clay) and a salinity of 25-30 $^{0}/_{00}$ (Eldridge *et al*., 1979).

---

[1] Technical contribution no. 2447, published by permission of the Director, S.C. Agriculture Experiment Station.

American Malacological Bulletin, Vol. 4(2) (1986): 149-155

Clams were measured and trays cleaned 9 times over a 4.5 year period from January 1976 through May 1980. Each surviving clam was measured for SL, SH and SW, and if necessary, clams were renumbered with a felt-tip pen. Great care was taken to maintain the identity of individual clams. Clams that died during the study period were not replaced, but the numbers on their empty shells were recorded as an identity check on surviving clams.

Linear measurements were computed and compared using Statistical Analysis Systems (SAS-79) (Barr *et al.*, 1979). Specific statistical procedures (regression analysis, correlation coefficients, Kolmogorov's D statistic and χ^2 tests) used to analyze data are noted in the following section.

RESULTS

The means and standard deviations of the three shell dimensions measured are shown in Figure 1. The three shell dimensions exhibit similar growth patterns, and the relationships of SW and SH regressed against SL were linear (R^2 for $^{SH}/SL$ = 0.97; R^2 for $^{SH}/SL$ = 0.99). Since the shell proportions did not change over SL ranges used in this study, and SL has been extensively used in the past to report growth in *M. mercenaria* (Ansell, 1968 and references within), it was selected for further statistical analysis and presentation of results.

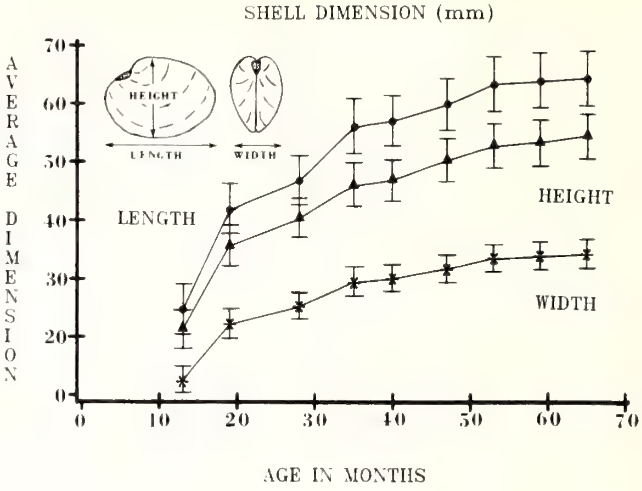

Fig. 1. Mean and standard deviations of shell length, height and width for clams grown in a subtidal location in South Carolina from January 1976 to May 1980. All shell dimensions in mm.

The number of surviving clams and the respective size distributions are shown in Figure 2. The calculated instantaneous mortality rate (Z) was 0.04, which translates into annual mortality rate 4.06% (Ricker, 1975). Approximately 50% of the total mortality, occurred in the interval between April and November, 1977. Nothing unusual happened during this time interval to explain the high mortality. It is possible

Table 1. Size-specific mean growth rates (Δ SL/month) by time intervals (age in months) for clams (N = 266) grown in a subtidal location in South Carolina from January 1976 to May 1980. Number of clams in each size-class interval in parenthesis.

Initial Size (mm)	Jan-Jul 1976 (13-19)	Jul-Apr 1977 (19-28)	Apr-Nov 1977 (28-35)	Nov-Apr 1978 (35-40)	Apr-Nov 1978 (40-47)	Nov-May 1979 (47-53)	May-Nov 1979 (53-59)	Nov-May 1980 (59-65)	Mean (13-65)
< 25.0	2.94 (130)								2.94 (130)
25.0-29.9	2.74 (111)								2.74 (111)
30.0-34.9	2.72 (24)	0.57 (11)	1.41 (2)						2.01 (37)
35.0-39.9	2.65 (1)	0.55 (67)	1.38 (7)						0.66 (75)
40.0-44.9		0.52 (130)	1.34 (83)	0.28 (1)	0.38 (1)				0.83 (215)
45.0-49.9		0.54 (50)	1.35 (119)	0.33 (21)	0.51 (11)	0.50 (4)	0.67 (1)	0.05 (1)	0.98 (207)
50.0-54.9		0.44 (8)	1.37 (48)	0.24 (92)	0.44 (81)	0.58 (31)	0.18 (7)	0.02 (4)	0.54 (271)
55.0-59.9			1.31 (7)	0.15 (94)	0.38 (108)	0.60 (103)	0.09 (57)	0.03 (45)	0.32 (414)
60.0-64.9				0.08 (47)	0.38 (52)	0.57 (90)	0.12 (102)	0.05 (103)	0.23 (394)
65.0-69.9				0.04 (11)	0.46 (13)	0.59 (34)	0.13 (75)	0.06 (83)	0.18 (226)
> 69.9						0.45 (4)	0.12 (24)	0.04 (30)	0.10 (58)
Mean	2.84 (266)	0.53 (266)	1.35 (266)	0.18 (266)	0.41 (266)	0.58 (266)	0.12 (266)	0.05 (266)	

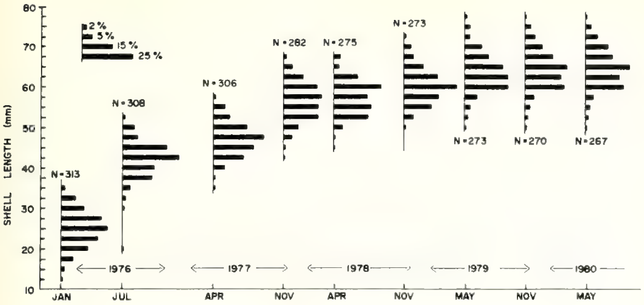

Fig. 2. Histograms show size (shell length) distributions of clams grown in a subtidal location in South Carolina from January 1976 to May 1980. Population size (N) listed adjacent to the histograms.

that some of the mortality was related to the sampling procedure, because April 1977 was the first time that clams were stored in a refrigerated room out of water during the measuring process. During the previous measuring periods, clams were stored in saltwater aquaria. Some stress may have been associated with the transfer of clams from ambient water temperatures of 18-20°C to refrigerated room temperatures of 12-13°C and back to ambient temperatures over a 3-day period.

Of the 267 clams that survived to the end of the study, 266 clams had complete growth records. The individual with incomplete growth records was deleted from the data base and further statistical analysis. Growth (Δ SL/month) declined over the 4.5 year study period (Table 1). The first (Jan-Jul 1976) and the third time intervals (Apr-Nov 1977) had the greatest monthly incremental increase in SL.

Comparisons of growth (Δ SL/month) between size-class intervals within any time interval (columns in Table 1) indicated a general decrease with increased size. Growth was also observed to decrease with increased age. Comparisons of growth of the same size clams (e.g. 40.0-59.9 size-class

Table 2. Distribution (%) of 5-size categories by sampling data (age in months) for clams grown in a subtidal location in South Carolina from January 1976 to May 1980. Initial classification of size categories of class based on shell length at planting (Jan 1976).

Size Categories		Jan 1976 (13)	July 1976 (19)	Apr 1977 (28)	Nov 1977 (35)	Apr 1978 (40)	Nov 1978 (47)	May 1979 (53)	Nov 1979 (59)	May 1980 (65)
	VS	100	69.8	62.3	47.2	43.4	35.8	26.4	28.3	28.3
Very Small	S	-	28.3	26.4	32.1	30.2	32.1	35.8	34.0	37.7
Clams	M	-	1.9	7.6	9.5	11.3	13.2	17.0	15.1	13.2
(VS)	L	-	0.0	1.9	7.6	11.3	11.3	9.4	9.4	7.6
	VL	-	0.0	1.9	3.8	3.8	7.6	11.3	13.2	13.2
	VS	-	22.6	34.0	32.1	34.0	34.0	34.0	32.1	34.0
Small	S	100	45.3	35.8	35.8	32.1	26.4	24.5	20.8	18.9
Clams	M	-	30.2	26.4	17.0	13.2	26.4	18.9	22.6	22.6
(S)	L	-	1.9	3.8	15.1	20.8	9.4	20.8	22.6	22.6
	VL	-	0.0	1.9	0.0	0.0	3.8	1.9	1.9	3.8
	VS	-	7.6	3.8	13.2	13.2	11.3	17.0	17.0	17.0
Medium	S	-	17.0	22.6	13.2	13.2	24.5	17.0	22.6	20.8
Sized	M	100	37.7	34.0	28.3	28.3	18.9	26.4	22.6	24.5
Clams	L	-	34.0	30.2	37.7	34.0	34.0	26.4	24.5	26.4
(M)	VL	-	3.8	9.4	7.6	11.3	11.3	13.2	13.2	11.3
	VS	-	0.0	0.0	3.8	7.6	7.6	7.6	7.6	7.6
Large	S	-	9.4	5.7	7.6	9.4	11.3	17.0	17.0	15.1
Clams	M	-	18.9	26.4	32.1	34.0	28.3	24.5	26.4	26.4
(L)	L	100	47.2	39.6	22.6	17.0	24.5	20.8	20.8	22.6
	VL	-	24.5	28.3	34.0	34.0	28.3	30.2	28.3	28.3
	VS	-	0.0	0.0	3.7	3.7	11.1	14.8	15.1	13.2
Very	S	-	0.0	11.1	11.1	14.8	5.6	5.6	5.6	7.6
Large	M	-	11.1	5.6	13.0	13.0	13.0	13.0	13.0	15.1
Clams	L	-	16.7	24.1	16.7	16.7	20.4	22.2	22.2	20.8
(VL)	VL	100	72.2	59.3	55.6	51.8	50.0	44.4	44.4	44.4
Chi^2 Value		-	292.02	204.4	140.95	115.89	88.17	62.56	58.04	63.01
d.f.		-	16	16	16	16	16	16	16	16
P.		-	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

Chi $^2(\chi^2)$ test of association.

intervals or rows in Table 1) between the third (Apr-Nov 1977) and fifth time interval (Apr-Nov 1978) indicated that younger clams grew faster, approximately 4 times faster than older clams. This trend was especially noticeable when growth of clams in the sixth (Nov 1978 - May 1979) and last interval (Nov 1979 - May 1980) were compared. Growth of the younger clams (i.e. during sixth interval) was 10 times that of the older clams during the last time interval.

The relative position of individual clams in the size distribution was followed throughout the study. Individual clams surviving the study period (N = 266) were grouped into one of 5-size categories (very small, small, medium, large, and very large clams) according to an individual's SL and position in the size distribution in January 1976 (age 13 months). Each size category was allocated equal number of clams (53 clams per category) so that the 53 smallest clams were categorized as very small, the next 53 clams as small, and so on. Table 2 gives the relative position (as a percentage) in the size distribution throughout the study of each of the initial size categories of clams. For example, clams classified as very small clams in January 1976 (100%) constituted 69.8% of the very small and 1.9% of the medium-sized clams in July 1976. By May 1980, only 28.3% remained in the very small category, while 13.2% were found among the very largest clams in the size distribution. Some very small and small clams caught up with larger individuals or compensated after 4.5 years of growth. However, a greater percentage of clams tended to maintain their relative positions in the size distribution. During the study, 24% and 19% of the individual clams remained within their respective size categories for 7 and 8 consecutive time intervals and 15% remained in their size category throughout the study. The χ^2 test of associa-

Table 3. Distribution (%) of 5-growth rate categories by time interval (age in months) for clams grown in a subtidal location in South Carolina from January 1976 to May 1980. Initial classification of clam growth rates based on rates between initial planting and first sampling data (Jan-Jul 1976).

Growth Rate Categories		Jan-Jul 1976 (13-19)	Jul-Apr 1977 (19-28)	Apr-Nov 1977 (28-35)	Nov-Apr 1978 (35-40)	Apr-Nov 1978 (40-47)	Nov-May 1979 (47-53)	May-Nov 1979 (53-59)	Nov-May 1980 (59-65)
	VS	100	20.8	28.3	13.2	26.4	28.3	26.4	24.5
Very Slow	S	-	20.8	20.8	13.2	13.2	26.4	24.5	15.1
Growing	I	-	18.8	20.8	22.6	24.5	17.0	11.3	9.4
Clams	F	-	17.0	15.1	28.3	15.1	13.2	17.0	15.1
(VS)	VF	-	22.6	15.1	22.6	20.8	15.1	20.8	35.8
	VS	-	15.1	24.5	20.8	20.8	20.8	20.8	20.8
Slow	S	100	28.3	20.8	28.3	18.9	18.9	24.5	20.8
Growing	I	-	13.2	20.8	15.1	28.3	15.1	24.5	28.3
Clams	F	-	26.4	22.6	15.1	17.0	24.5	20.8	20.8
(S)	VF	-	17.0	11.3	20.8	15.1	20.8	9.4	9.3
	VS	-	20.8	11.3	17.0	15.1	18.9	22.6	22.6
Intermediate	S	-	11.3	22.6	26.4	28.3	22.6	18.9	26.4
Growing	I	100	34.0	20.8	20.8	17.0	18.9	18.9	13.2
Clams	F	-	18.9	20.8	13.2	20.8	18.9	17.0	20.8
(I)	VF	-	15.1	24.5	22.6	18.9	20.8	22.6	17.0
	VS	-	22.6	17.0	24.5	20.8	17.0	15.1	20.8
Fast	S	-	20.8	18.9	17.0	17.0	13.2	13.2	15.1
Growing	I	-	18.9	26.4	24.5	17.0	24.5	24.5	22.6
Clams	F	100	22.6	18.9	17.0	20.8	24.5	24.5	24.5
(F)	VF	-	15.1	18.9	17.0	24.5	20.8	22.6	17.0
	VS	-	20.4	18.5	24.1	16.7	14.8	14.8	11.1
Very Fast	S	-	18.5	16.7	14.8	22.2	18.5	18.5	22.2
Growing	I	-	14.8	11.1	16.7	24.1	24.1	20.4	18.5
Clams	F	-	14.8	22.2	25.9	18.5	20.4	18.5	18.5
(VF)	VF	100	31.5	31.5	18.5	24.1	24.1	25.9	22.2
Chi^2 Values		-	19.45	16.18	14.85	12.94	10.88	13.47	23.94
d.f.		-	16	16	16	16	16	16	16
P.		-	0.246	0.440	0.536	0.677	0.817	0.836	0.091

Chi^2 (χ^2) test of association.

tion indicated that a significant ($P \leq 0.0001$) association existed between the initial size-category classification of clams and their relative position in the size distribution after growing for various time periods. Thus, it appeared, the size (SL) the majority of clams obtained by their first year's growth was an indicator of their position in the size distribution in future years.

In an attempt to determine if growth in a particular time interval was equally as good an indicator as size (SL) of future growth, 5 categories of growth (very slow, slow, intermediate, fast and very fast) were classified according to an individual clam's growth performance. Initially, the 5 categories were based on the growth in the first time interval (Jan-Jul 1976) and traced through the remainder of the study period (Table 3). As a follow-up to these analyses, growth performance of individual clams were similarly scored, but an individual's growth category was reclassified according to its growth in the immediately preceding time interval so that the growth rate classification based on a single time interval did not bias our conclusions. Results from these analyses were almost identical to those done initially, and therefore, were not presented in tabular form. The χ^2 test values of association listed in Table 3 indicated little association existed between growth in the first time interval (or any time interval) and growth in another interval. For example, clams which were very slow growers in the first time interval (Jan-Jul 1976) were distributed almost equally among the other growth categories (slow, intermediate, fast and very fast) by the next and following time intervals. Only 1.5% and 0.4% of the clams remained within their respective growth categories for 4 and 5 consecutive intervals; none remained in the same growth category after 6 consecutive intervals. An increased association indicated by a higher χ^2 value in the last time interval probably resulted from difficulties in determining which clams were slow and very slow growers when growth had slowed to a negligible rate (see Table 1).

Table 4. Mean initial shell length (SL in mm) and changes in SL (Δ SL) by time interval for the very slowest growing ($N = 53$) and very fastest growing clams ($N = 53$) held in a subtidal location in South Carolina from January 1976 to May 1980. Growth rate categories based on clams performance in the preceding time interval.

Time Intervals (age)	Very Slow Growers		Very Fast Growers	
	$\bar{X}$ SL ± SD	$\bar{X}$ ΔSL ± SD	$\bar{X}$ SL ± SD	$\bar{X}$ ΔSL ± SD
Jan-Jul 1976 (13-19)	25.8 ± 4.17	14.0 ± 1.12	23.0 ± 4.28	20.2 ± 0.97
Jul-Apr 1977 (19-28)	42.7 ± 3.46	2.4 ± 0.66	41.5 ± 4.50	7.2 ± 0.93
Apr-Nov 1977 (28-35)	46.8 ± 4.24	6.7 ± 0.84	46.5 ± 4.64	12.4 ± 1.05
Nov-Apr 1978 (35-40)	59.0 ± 3.74	n.d.	53.9 ± 4.04	2.5 ± 1.04
Apr-Nov 1978 (40-47)	57.1 ± 4.11	1.0 ± 0.42	56.0 ± 4.47	5.0 ± 1.07
Nov-May 1979 (47-53)	60.3 ± 5.06	1.7 ± 0.54	59.6 ± 4.97	5.4 ± 0.61
May-Nov 1979 (53-59)	62.6 ± 4.72	0.1 ± 0.05	64.7 ± 4.48	1.8 ± 0.65
Nov-May 1980 (59-65)	62.9 ± 4.94	n.d.	65.1 ± 4.24	1.0 ± 0.39

n.d. = no detectable growth.

Mean SL and growth (ΔSL) of the very slow growing and very fast growing categories of clams ($N = 53$/category) in each time interval are presented in Table 4. Individual clams in the very slow and very fast categories change their status from one time interval to the next, so the mean changes in SL cannot be simply added to the mean SL in one time interval to yield the mean SL in another interval. Very fast growing clams were consistently smaller than very slow growers through May 1979 (53 months age). Examination of Figure 2 indicated a slight departure from a normal distribution of SL at this time, but this departure was nonsignificant ($P > 0.05$) according to Kolmogorov's D statistic. Clams averaged approximately 60 mm SL at 53 months of age (Fig. 1).

DISCUSSION

Annual mortality rate of 4.06% approximates a previous estimate (1.43%) for larger clams held under similar conditions (Eldridge and Eversole, 1982). In both studies, experimental trays were covered with a plastic cloth to help protect clams from predators so these figures underestimate mortality. However, what these studies do indicate is that mortality of clams (≥ 24 mm SL) is quite low in absence of predation. Other potential mortality factors such as Hurricane David which moved up the coastline of South Carolina in September 1979 had little effect on survival of clams in the subtidal location. On the other hand, clams held in one experimental tray in an intertidal location as part of another study, approximately 15 m from the subtidal location and 0.3 m above mean low water, experienced nearly 100% mortality during Hurricane David (Eldridge and Eversole, 1982).

Decreased incremental growth with increased size (SL) has been reported for hard clams (e.g. Chestnut, 1952; Gustafson, 1955; Pratt and Campbell, 1956). However, contrary to previous studies, growth (ΔSL) of clams also appeared to decrease with age. The mechanisms suggested for reduced growth with increases in bivalve size (e.g. reduced gross growth efficiency, Bayne *et al.*, 1976) have not been adequately explored to explain growth reductions with increases in age or the possible interaction between age and size. Senility itself does not appear to be principal cause for reduced growth with increases in age, because growth in long-lived bivalves such as hard clams continue throughout life (Comfort, 1979 and references within).

Shell growth which is known to be highly variable in molluscs (Wilbur and Owen, 1964), has been observed to gradually decline in variability with age and/or size of bivalves (Weymouth *et al.*, 1931; Kristensen, 1957; Walne, 1958; Brown *et al.*, 1976; Wendell *et al.*, 1976). The decline has been attributed to either growth compensation (Ricker 1969) or greater mortality at the extremes of the size distribution (Brown *et al.*, 1976). Mortality in this study, however, was not restricted to any particular age or size, partly because the clams were protected from predators.

According to Ricker (1975), a negative correlation between growth and initial size indicates growth compensation or the process where smaller individuals catch up with larger individuals in an age class. Correlations coefficients between the variables of initial size and incremental growth (Δ shell dimension) were negative (-0.439 for SL; -0.435 for SH; and -0.443 for SW). If smaller clams were catching up with larger clams, the standard deviation about mean linear shell measurements shown in Figure 1 would be expected to diminish with age and growth. The standard deviations in this study, however, were relatively constant or increased slightly (e.g. the standard deviation for SL increased from 4.19 to 4.82 over the 4.5-year study period).

The degree of compensatory growth exhibited in this study can occur without a decrease in standard deviation because not all the small clams caught up with larger clams in the study period (4.5 years). Data in Table 2 show that a considerable proportion of those clams starting as very large, large, intermediate, small and very small clams occupy the same size category after 4.5 years growth. The range of sizes also remains very similar over the study period with a slight skewness in the size distribution toward larger sizes after May 1979 (Fig. 2). After May 1979, the SL of the very fast growers were larger than the slowest growers (Table 4). This may be the point (age and size) where some clams finally compensate for delayed initial growth and catch up with those clams with a head start on growth.

Evidence of this sort suggests that compensatory growth in molluscs may be more common place than previously thought. Those investigations where decreases in standard deviation have been reported (e.g. Kristensen, 1957; Walne 1958) were probably the most dramatic cases of growth compensation, if size selective mortality can be assumed not to be the principal causative factor. Crabs appear to exhibit some size selection when preying on hard clams (Whetstone and Eversole, 1978, 1981). A more complete picture of compensatory growth in molluscs relies on a good (valid) aging technique, a problem that has plagued malacologists for years, and a method of back calculation of body dimension similar to that used with fish (e.g. Carlander, 1981). Development of the acetate peel method of preparing shell sections (Rhoads and Lutz, 1980) and validation of this aging technique with bivalves (e.g. Ropes, 1984) will go a long way in resolving the problem of compensatory growth in molluscs.

As expected, individuals in designated shell-size categories (Table 2) remained quite constant where individuals in growth rate categories continuously changed during the study (Table 3). Shell size is a history of past growth events and is less likely to change abruptly. Growth which is a dynamic process is continually being influenced by and responding to environmental, physiological and genetic factors. For example, Chanley (1959) observed that individual clams of similar genetic background grew well in one year and, then poorly in another year. He attributed this variation in shell growth to environmental factors, even though clams were reared under nearly identical conditions. Apparently, individual clams can rapidly change growth rates in response to microenvironmental factors which may not be readily obvious to the researcher. In our case, filtration rates and food uptake of individual clams may have been influenced by their position in the tray (e.g. edge vs. centrally located planting positions) which in turn could have influenced the growth of an individual.

Since clams were virtually the same age, differences in initial SL in January 1976 must have resulted from more rapid growth of some individuals during the growout phase from May 1975 to January 1976. Shell growth of individuals varied considerably over this 8-month period prior to marking in January. For example, at May 1975, a sample of 400 clams ranged from 9.9-16.8 mm SL and had mean SL of 13.0 mm (SD = 1.43) compared to a range of 11.7 to 35.3 mm SL and mean SL of 24.7 mm (SD = 4.19) in January 1976. If these differences in growth rate are due in part to genetic factors, then growth (size) could be used in designating individuals for selective breeding programs. The existence of growth differences at this size range or age, however, does not appear to provide the appropriate information from which to make the most reliable selections. Selection of the top 20% of the population, as fast growers when clams average 25 mm SL (and approximately 1 year of age) could result in considerable error. It is noteworthy, that less than 50% of the clams categorized as very large clams in January 1976 were very large after May 1979 (53 months of age) (Table 2). Also 33% of those originally classified as very large had growth such that they assumed positions in the size distribution equivalent to the intermediate, small and very small size categories by 53 months (Table 2).

Our data does not permit recommendations concerning specific size at which to begin picking the fastest growers for a selective breeding program. The probability of selecting the fastest growers increases with time and growth of clams, but it would be impractical and expensive for clam breeders to wait until clams reached 60 mm SL (and age of approximately 4 years in our situations) before selecting the fastest growers. Ideally, the selection process should be targeted for those clams which reach market size (approximately 45 mm SL) the fastest. We feel this may be best accomplished by selecting the fastest growers after clams have completed the rapid growth phase and have, hopefully, compensated for any slow start.

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SENTENTĬA

THE RELEVANCY OF THE GENERIC CONCEPT TO THE GEOGRAPHIC DISTRIBUTION OF LIVING OYSTERS (GRYPHAEIDAE AND OSTREIDAE)

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ABSTRACT

Since 1758, numerous species of living oysters have been named, mostly in the genus *Ostrea*. Beginning in the 1930's, more extensive anatomical investigations resulted in the acceptance of more genera, improved definition of taxa, and a great reduction in the number of accepted specific names. Presently the 36 recognized species are distributed among 24 genera and subgenera. These species are so distributed geographically that only one species of a genus (or subgenus) occurs in a given area. An area is here defined as one latitudinal climatic zone of a province, the latter being longitudinal regions of shallow water separated alternately by continental masses and broad areas of deep water. As now restricted, genera consist of either two or more allopatric species, or a single species so distinct that it does not have a geminate species in another area. These morphological and distributional limits of genera are probably valid for other shallow water benthic marine mollusks, few groups of which have had exhaustive generic analysis based on extensive comparative anatomical studies within a family.

The taxonomic history of molluscan genera which were introduced in the 18th century can usually be divided into three stages. In the initial stage, a genus was introduced, with few to many species; there was no conscious recognition of types, nor families or other categories between genus and order. The second stage was one of generic expansion, during which many additional species were named in each of the few recognized genera. More categories and the type concept were introduced, usually with vague application. The third stage was one of generic analysis and restriction; the number of genera was increased, but now each had only one or a few species; the type concept was more rigorously applied. Several more categories were introduced, including suborder, superfamily, tribe and subgenus. The taxa were more precisely defined through extensive comparative anatomical studies, distribution and behavior.

The taxonomic history of oysters exemplifies these stages very well (Table 1). When Linné (1758) proposed a list of oysters in the tenth edition of the Systema Naturae, he included several species of bivalves in the genus *Ostrea* which would not be considered true oysters today, and some of the true oysters that he first described he put in the genera *Mytilus* and *Anomia*.

Other authors of the late 18th century (e.g. Born, 1778; Gmelin, 1791) continued to use the system of Linné, introducing new species of oysters in the genus *Ostrea*. In the early part of the 19th century Lamarck (1815-1822) made important revisions in the system of Linné. In the case of oysters, he removed several groups from *Ostrea* to other genera, notably *Pecten, Malleus, Placuna*, etc., and he transferred the species of oysters which Linné had put in other genera to *Ostrea*. He also named many new species in that genus. For the rest of the 19th century authors continued to add to the list of oysters, nearly always placing the new species in the genus *Ostrea*. Other genera were introduced, but not widely used, and none had its limits well defined anatomically.

There was an intensified interest in oyster systematics during the 1930's, with several authors approaching the subject in different ways. Lamy (1929-1930) compiled and evaluated the nominal species of oysters which had been proposed; Orton (1928) stressed the distinction between those oysters which are larviparous and those which are oviparous, and Nelson (1938) showed that there is a major morphological difference between the two groups; Vyalov (1937) introduced several new genera and subgenera, and recognized four subfamilies (two extinct), but his proposals were not immediately accepted; instead, the influence of Ranson (1943) prevailed, and all living species were distributed among three genera, in one family, without subfamilies or other divisions: *Pycnodonte, Ostrea* and *Crassostrea*. Several papers of the

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Table 1. Summary of the conceptual history of classification of the oysters, families Gryphaeidae and Ostreidae. The names of authors in the top row indicate those most responsible for the developments in generic expansion at the time below their names, and the dates. At the bottom of the table the general state of taxonomic procedure is indicated, as exemplified in the work of the authors cited.

HISTORY OF GENERIC EXHAUSTION IN TRUE OYSTERS
(GRYPHAEIDAE AND OSTREIDAE)

Linnaeus	Lamarck	Lamy Nelson Orton Ranson Vyalov	Stenzel	Torigoe Harry
1758	1819	1930's	1971	1981- 1985
OSTREA (Included true oysters plus many others) *MYTILUS* (Included three true oysters *ANOMIA* (Included one fossil oyster)	*OSTREA* (Genus limited to true oysters; those in *MYTILUS* also placed here)	*OSTREA* *CRASSOSTREA* *PYCNODONTE*	*HYOTISSA* *NEOPYCNODONTE* *OSTREA* *SACCOSTREA* *STRIOSTREA* *CRASSOSTREA* *LOPHA* *ALECTRYONELLA* *(ANOMIOSTREA)*	*HYOTISSA* *PARAHYOTISSA* *P. (PLIOHYOTISSA)* *P. (NUMISMOIDA)* *NEOPYCNODONTE* *LOPHA* *ALECTRYONELLA* *DENDOSTREA* *MYRAKEENA* *ANOMIOSTREA* *OSTREOLA* *OSTREA* *O. (EOSTREA)* *NANOSTREA* *PLANOSTREA* *CRYPTOSTREA* *TESKEYOSTREA* *BOONEOSTREA* *PUSTULOSTREA* *UNDULOSTREA* *SACCOSTREA* *STRIOSTREA* *S. (PARASTRIOSTREA)* *CRASSOSTREA*
NO FAMILIES NO SUBFAMILIES NO TRIBES NO SUBGENERA	ONE FAMILY NO SUBFAMILIES NO TRIBES NO SUBGENERA	ONE FAMILY NO SUBFAMILIES NO TRIBES NO SUBGENERA	TWO FAMILES FIVE SUBFAMILIES (2 extinct) NO TRIBES (in living Oyst.) NO SUBGENERA	TWO FAMILIES FOUR SUBFAMILIES TEN TRIBES SUBGENERA RECOGNIZED

next three decades adopted that system (Thompson, 1954; Galtsoff, 1964); however, the authors of faunal catalogues were more conservative, referring nearly all living oysters to the single genus *Ostrea* (McLean, 1941; Olsson, 1961; Keen, 1971).

Stenzel (1971) made a major revision of the systematics of oysters and attempted to unify the subject by extending the generic analyses to both fossil and recent species. He accepted numerous genera proposed by Vyalov and earlier workers, besides proposing a few himself, and he recognized two families and five subfamiles (two extinct). He distributed the living oysters among nine genera (Table 1). However, only the type species were considered in any detail by Stenzel, who illustrated and described them extensively, with strict application of the type concept.

Therefore there remained the problem of allocating all other living species of oysters, which are not types of genera, to the genera which he recognized. A first step was to use the more reliable faunal lists of selected areas, such as those of McLean (1941) for the Western Atlantic, and Olsson (1961) and Keen (1971) for the Eastern Pacific. The process was augmented by studying the extensive collection of oysters at the U.S. National Museum of Natural History, the British Museum of Natural History, the Houston Museum of Natural Science and several large private collections. Studying the flesh of oysters, as well as more careful attention to shell characters, resulted in more exact definitions of taxa. Several new taxa were recognized, at the level of subgenus, genus, tribe and subfamily, to explain the relationships and diversity of oysters more exactly (Harry, 1985).

Torigoe (1981), whose study was limited to the living oysters of Japan, independently found several new anatomical characters which are useful in systematics. He named one new subfamily, Crassostreinae, but no taxa at lower levels.

From the standpoint of faunal distribution of the taxa, it soon became evident that every species of a given area belongs to a different genus or subgenus; or, by logical conversion of this proposition: a genus or subgenus is represented in a given area by only one species. This does not preclude the possibility of a species extending into more than one area, and indeed it implies that genera may do so. The principle will be more easily understood if we understand the meaning of the terms genus and area, as they are used here.

In studying the distribution of shallow water benthic marine molluscs, six major regions are generally recognized (Fig. 1). Four are longitudinal, and these we may call provinces: Eastern Atlantic, Western Atlantic, Eastern Pacific and Indo-Western Pacific. The two latitudinal regions, which we may call zones, are the Arctic and Antarctic. The natural boundaries of these provinces and zones are formed by things which constitute distributional barriers, and they are of three kinds. The longitudinal barriers are alternating continental masses and broad areas of deep water. The two latitudinal zones are separated not only by great distance, but also by temperature gradients along the provinces.

The provinces can be subdivided by regimes of light and temperature variation, and these might be exactly limited by the Arctic and Antarctic Circles and the Tropics of Cancer and Capricorn, except for the presence of major oceanic currents. Around Antarctica the water moves in a single current, from west to east; it is uniformly cold, throughout the year. No comparable current serves as a barrier in the Arctic Ocean, where the shallow water region is along the northern shores of Eurasia and North America, and the ocean is separated from the others by a narrow passage into the Pacific and a broader one into the Atlantic Ocean. In

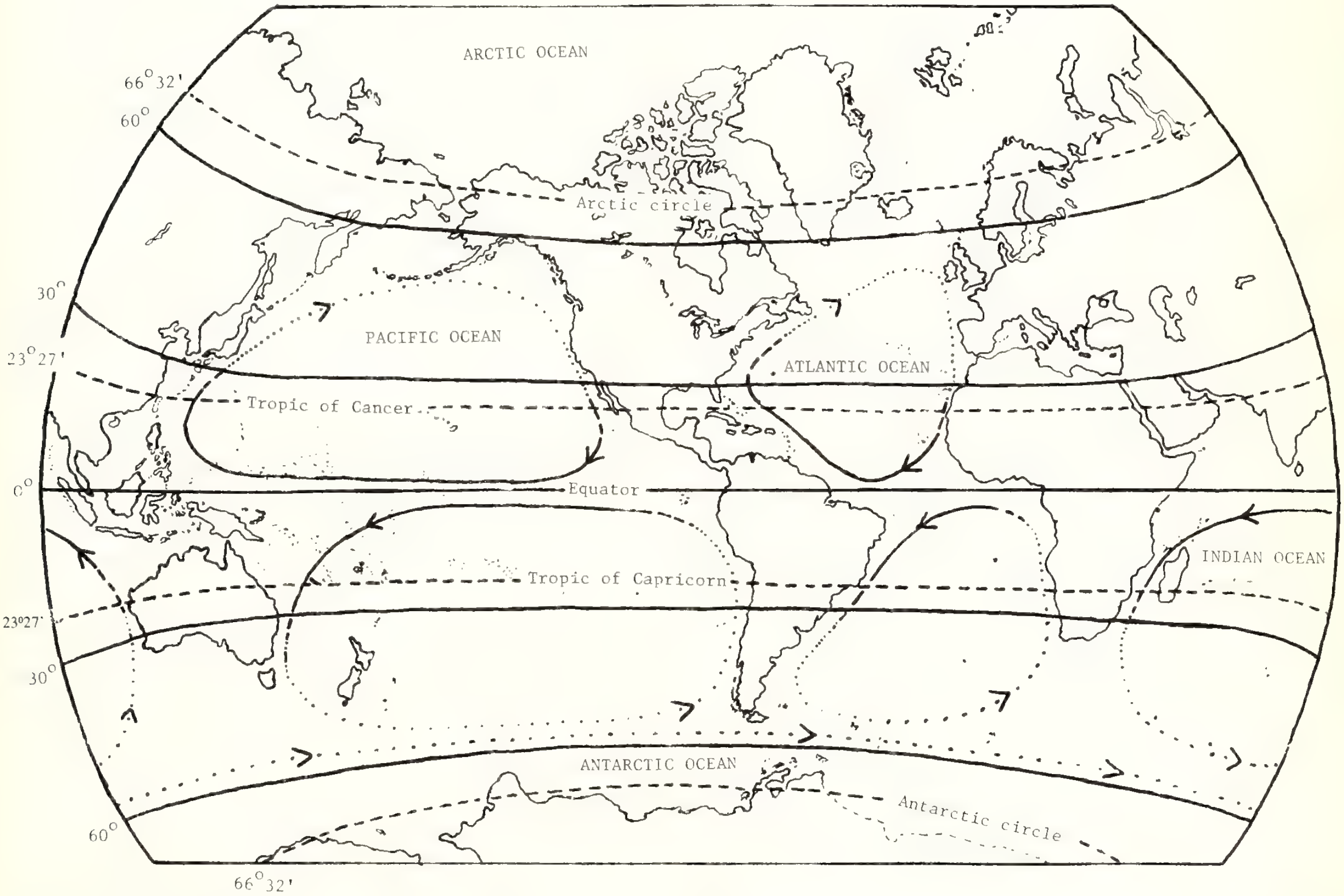

Fig. 1. Map of the world, showing the latitudes bounding climatic zones (labeled: Arctic and Antarctic Circles, Tropics of Cancer and Capicorn), and the effect of major ocean currents in shifting the real thermal boundaries of those zones. Arrows on the lines indicating oceanic currents show direction of movement; continuity of those lines indicate temperature; the continuous part of each line representing the warmer part of a current, with the cooler part being dotted.

temperate and tropical latitudes, the major ocean currents form large gyres. They take up heat in the low latitudes, and release it gradually in higher ones. Thus they act as giant heat distributors, because water heats and cools more slowly than air or land. The gyres distort the climatic zones on all continental coasts. In the northern hemisphere the gyres move clockwise, whereas those of the southern hemisphere move in the opposite direction. Consequently the climate of a given latitude in the temperate zones is warmer on the eastern than on the western margin of a continental mass.

The range of temperature in which each species occurs varies with the species, and it is impractical, for present purposes, to define the subzones of the provinces precisely; these subzones are, from north to south: Northern Cool Temperate, Northern Warm Temperate, Tropical, Southern Warm Temperate and Southern Cool Temperate. An area, for purposes of applying the principle stated above, is one climatic zone of a province.

The distribution of the 36 species of living oysters which I can presently recognize are shown in Table 2. No species occurs in the Arctic or Antarctic zones, which are therefore omitted.

All genera but one are represented in the tropics. One species, *Neopycnoconte cochlear* (Poli, 1795) is nearly world wide in distribution, although localized and infrequently taken; this reaches the greatest depth of any oyster, 2100 m, and although it has been found as shallow as 27 m, a depth attained and exceeded by a few other species, most of the records of this oyster are from below 200 m, a depth not reached by other species. It has not been found in the Eastern Pacific province. A shallow water species, *Ostrea (Eostrea) puelchana* Orbigny, 1846, is also world wide, but will be dealt with below.

Several species of oysters occur in two adjacent provinces, as follows: *Hyotissa hyotis* (Linné, 1758) in the Indo-Western Pacific and Eastern Pacific; *Parahyotissa mcgintyi* (Harry, 1985) in the Western Atlantic and Eastern Atlantic; *Dendostrea frons* (Linné, 1758) in the Western Atlantic and Eastern Atlantic; and *Saccostrea cucullata* (Born, 1778) in the Eastern Atlantic and Indo-Western Pacific.

Seventeen of the 24 genera and subgenera are monotypic; excepting the three noted above, *N. cochlear, H. hyotis* and *O. (E.) puelchana,* their species are limited to one province, and often to a very small part of that province. That leaves seven genera and subgenera with species ranging from two to four in number; of these, no genus or subgenus has more than one species in a given province: *Parahyotissa, Dendostrea, Ostreola, Ostrea s. s., Saccostrea, Striostrea s. s.* and *Crassostrea*. If one examines the species of those genera and subgenera, one finds that the species are extremely similar to each other. They are what are generally called analogous species. Several other terms are used to designate this close similarity of species of different provinces, notably allopatric species, geminate or twin species, homologous species, vicarious species and cognate species.

The concept of genus in oysters probably should be restricted to analogous species as the latter are thus defined. Or, if a species has no close analogue in another province, it should be recognized as a monotypic genus (or subgenus, depending on the degree of difference from other species most similar to it). The hesitation and qualification of these assertions are deliberate, because genera and species should ultimately be differentiated on a morphological basis, to which the distinctness in distribution is secondary. Morphological differences among all genera and subgenera of oysters here recognized have been found (Harry, 1985).

Species of a few genera, notably *Ostreola* and *Crassostrea*, extend from the Tropical through the Warm Temperate and even to the Cool Temperate zones. One genus of oysters that does not live in the Tropical, or even within the Warm Temperate zone, is the genus *Ostrea* as restricted by my studies. It has only three species, but in two subgenera. *Ostrea s.s.* has two species, broadly separated; both occur in the northern hemisphere, approximately between the latitudes 35° and 60° north, on the coasts of Europe (*O. edulis* Linné, 1758) and Asia and Japan (*O. denselamellosa* Lischke, 1869). These are most abundant at several meters depth, but an occasional specimen occurs in the low intertidal area. The third species, *O. (E.) puelchana,* occurs around the world in the southern hemisphere between latitudes 35° and 50° south. It is found on both coasts of South America, the southern island of New Zealand, the southern coast of Australia, off South Africa, and at some smaller islands. Oddly, no species of true *Ostrea* as presently defined lives naturally on the coasts of North America.

Thus, genera are not present in all areas where they might be expected, on the basis of climatic preference of their species elsewhere. *Saccostrea* and *Striostrea* are absent from the Western Atlantic, but present in the other three provinces. A very interesting case is *Ostreola*. It is not present in the Indo-Western Pacific province, where two monotypic genera closely related to it occur. One is *Nanostrea*, a dwarf oyster which seems to lead to three monotypic genera placed in Cryptostreini, the species of which are small, reclusive and with reduced features. The other is *Planostrea*, which in many ways is the tropical counterpart of *Ostrea*, intermediate between it and *Ostreola*.

Is the principle of 'only one species of a genus in an area' applicable to molluscs other than oysters? A cursory examination of some of the more extensive systematic works on other families suggests that it is, at least for some. As data are accumulated, very likely some modifications or limitations of the maxim's applicability will be found necessary. One obvious limitation is the habitat of the molluscs involved. The principle may be limited in the marine environment to shallow water, benthic molluscs, i.e., those living in or near the substrate, in less than 200 m depth. This excludes pelagic and abyssal species, whose environment is more uniform, and with fewer isolation barriers.

A prerequisite for applying the principle is that an exhaustive study of the species of a family must have been made, and genera determined on the basis of extensive anatomical examination. This has been done on surprisingly few mollusc groups, especially among marine ones. Certainly few marine groups have been as thoroughly explored anatomically as the Unionidae of fresh water, and the ter-

Table 2. Systemic distribution in families, subfamilies and tribes of the living oysters are in the three columns on the left of the genera and species. On the right the distribution of each species is shown in the five climatic zones of the four provinces recognized. The provinces are: I.W. Pac - Indo-Western Pacific; E. Pac. - Eastern Pacific; W. Atl. - Western Atlantic; E. Atl. - Eastern Atlantic. The zones are: N.C. - Northern Cool Temperate; N.W. - Northern Warm Temperate; TROP. - Tropical; S.W. - Southern Warm Temperate; S.C. - Southern Cool Temperate.

FAMILY	SUBFAM.	TRIBE	GENUS AND SPECIES	I.-W. Pac.					E. Pac.					W. Atl.					E. Atl.				
				N.C.	N.W.	Trop	S.W.	S.C.	N.C.	N.W.	Trop	S.W.	S.C.	N.C.	N.W.	Trop	S.W.	S.C.	N.C.	N.W.	Trop	S.W.	S.C.
GRYPHAEIDAE	PYCNODONTEINAE	HYOTISSINI	*HYOTISSA HYOTIS* (Linne, 1758)			X					X												
			PARAHYOTISSA MCGINTYI Harry, 1985												X	X					X		
			P. IMBRICATA (Lamarck, 1819)			X																	
			P. (PLIOHYOTISSA) QUERCINUS (Sowerby, 1871)							X	X												
			P. (NUMISMOIDA) NUMISMA Lamarck, 1819)			X																	
		N.	*NEOPYCNODONTE COCHLEAR* (Poli, 1795)		X	X	X								X					X			
OSTREIDAE	LOPHINAE	LOPHINI	*LOPHA CRISTAGALLI* (Linne, 1758)		X	X																	
			ALECTRYONELLA PLICATULA (Gmelin, 1791)		X	X																	
			DENDOSTREA FOLIUM (Linne, 1758)		X	X																	
			D. FRONS (Linne, 1758)												X	X	?				X		
			D. MEXICANA (Sowerby, 1871)							X													
		M.	*MYRAKEENA ANGELICA* Rochebrune, 1895)							X													
			ANOMIOSTREA CORALLIOPHILA Habe, 1975			X																	
	OSTREINAE	OSTREINI	*OSTREOLA STENTINA* (Payraudeau, 1826)																	X	X	?	
			O. EQUESTRIS (Say, 1834)												X	X	X	?					
			O. CONCHAPHILA (Carpenter, 1857)						X	X	X	?											
			OSTREA EDULIS Linne, 1758																X				
			O. DENSELAMELLOSA Lischke, 1869	X																			
			O. (EOSTREA) PUELCHANA Orbigny, 1846					X					X					X					X
			NANOSTREA EXIGUA Harry, 1985			X																	
			PLANOSTREA PESTIGRIS (Hanley, 1846)			X																	
		CRYPT.	*CRYPTOSTREA PERMOLLIS* (Sowerby, 1871)												X	?							
			TESKEYOSTREA WEBERI (Olsson, 1951												X	X							
			BOONEOSTREA CUCULLINA (Deshayes, 1836)			X																	
		P.	*PUSTULOSTREA TUBERCULATA* (Lamarck, 1804)			X																	
		U.	*UNDULOSTREA MEGODON* (Hanley, 1846)								X												
	CRASSOSTREINAE	STRIOSTREINI	*SACCOSTREA CUCULLATA* (Born, 1778)		X	X	X													?	X	?	
			SACCOSTREA PALMULA (Carpenter, 1857)							X	X												
			STRIOSTREA MARGARITACEA (Lamarck, 1819)																		X	X	
			S. PRISMATICA (Gray, 1825)								X												
			S. CIRCUMPICTA (Pilsbry, 1904)		X	?																	
			S. (PARASTRIOSTREA) MYTILOIDES (Lamarck, 1819)		?	X																	
		CRASS.	*CRASSOSTREA VIRGINICA* (Gmelin, 1791)											X	X	X	?						
			C. ANGULATA (Lamarck, 1819)																	X	X		
			C. COLUMBIENSIS (Hanley, 1846)							X	X												
			C. GIGAS (Thurnberg, 1793)	X	X	X																	

restrial helicoid snails. A century ago the species of those two groups were nearly all put in the genera *Unio* and *Helix*, respectively, each with a very large number of species. Extensive anatomical investigations led to the large number of genera presently recognized, with relatively few species in a genus.

I have found only one other study with exhaustive generic analysis, accompanied by extensive anatomical studies, which was done on marine bivalves. That is Turner's (1966) monograph of the Teredinidae. Although the distributional correlation is not presented in a simple fashion in that paper, when extracted it fits the principle proposed above very well. The few exceptions merit further attention.

Such studies must be on a world-wide basis, in groups which have such distribution. In recent years, most systematic monographs of families of marine molluscs have been limited to one province, as defined above, but some of those cite species of the genera they treat which occur in other provinces, and even correlate analogous species among provinces. Examples are Grau (1959) on the Pectinidae of the Eastern Pacific province, and several papers in the serial monographs, "Indo-Pacific Mollusks," particularly by Abbott (1960) on the genus *Strombus* and Rosewater (1970) on the Littorinidae.

Several statements were found in the literature which support the general idea, although they do not relate the obvious implications of the principle of generic limitation on a geographic basis to systematics and nomenclature in a practical way. In a paper on the origin of species in littoral prosobranchs, Fretter and Graham (1963) noted: "It is likely that speciation in the gastropods of marine habitats has been brought about primarily by means of geographic isolation. So little work, however, has been done upon this aspect of the evolution of the group, or indeed, of any group of marine invertebrates, that this statement of probability is as far as one should go. The only study of marine gastropods with this as one of its explicit aims—that of the cypraeids by the Schilders (1939)—concluded that speciation has been primarily allopatric and that the preceeding isolation was brought about by geographical barriers. Similarly Mayr (1954) concluded that allopatric speciation has been the only significant source of new species amongst echinoids."

The noted ichthyologist and first president of Stanford University, David Starr Jordan (1905), made a statement that approximates the formulation of the principle as presented in this paper even more closely: "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort."

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SYMPOSIUM ON THE ENCAPSULATION OF EMBRYOS BY MOLLUSCS

ORGANIZED BY

JAN A. PECHENIK
TUFTS UNIVERSITY

AMERICAN MALACOLOGICAL UNION
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THE ENCAPSULATION OF EGGS AND EMBRYOS BY MOLLUSCS: AN OVERVIEW

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ABSTRACT

Encapsulation of fertilized eggs within capsules or jelly masses is common among gastropods and cephalopods, and occurs rarely among bivalves. Understanding the selective pressures responsible for the evolution and present diversity of encapsulating structures and understanding the evolutionary history of encapsulation will require additional descriptive work and experimentation. The variety of approaches that can be taken to evaluate the evolutionary implications of encapsulation in shaping life history patterns is reviewed here.

Molluscan embryos commonly undergo at least a portion of their pre-juvenile development within some type of egg capsule or egg mass secreted by a specialized portion of the adult reproductive tract. Certainly, encapsulation is the rule rather than the exception among most gastropod families and among the cephalopods, and encapsulation appears sporadically among the bivalves. The eggs of chitons are enclosed in a complex "hull," but it is not clear whether these hulls are secreted by the oocytes themselves or by associated follicle cells (Pearse, 1979); in either case, the origins of these chiton egg coverings differ substantially from those of the other mollusc groups considered in this review. We should be careful to distinguish between well-formed, often leathery structures ("egg capsules") and gelatinous, sometimes amorphous structures ("egg masses"), and recognize that some species produce egg capsules embedded within gelatinous masses, so that, in such species, the term "egg mass" also includes the "egg capsules" lying within. Structures such as fertilization membranes, produced by the zygote rather than by the parental reproductive tract, should not be regarded as true egg capsules or egg masses.

The phenomenon of egg encapsulation has not been especially well studied despite its widespread occurrence within the Mollusca and its likely importance in shaping molluscan life history evolution. In this paper, I wish to 1) briefly consider the variety of approaches that have been used to study the phenomenon of encapsulation, 2) consider how each approach furthers our understanding of the forces shaping the evolution of encapsulation, and 3) indicate those areas in which further work is particularly needed and those approaches that might be especially profitable to pursue. As most of the following papers from the Encapsulation symposium are descriptive, I will briefly consider the descriptive approach in this paper but will focus my overview on other aspects of encapsulation biology.

DESCRIPTIVE APPROACH

Before one can talk about the evolution of one form from another, the forms must be described. What types of capsule or egg mass do different species make? What are the dimensions of the encapsulating structures? What are the structures made of? How are they made? How many embryos are contained in each capsule or mass? At what size and stage of development do the youngsters emerge?

A fair amount of such descriptive work has been published (e.g., Drew, 1901; Andrews, 1935; Graham, 1941; Thorson, 1946; Knudsen, 1950; Giglioli, 1955; Kohn, 1961; Ockelmann, 1962, 1964; Oldfield, 1964; Hurst, 1967; D'Asaro, 1970; Gibson *et al.*, 1970; Borkowsky, 1971; Houbrick, 1973; Radwin and Chamberlain, 1973; Buckland-Nicks and Chia, 1973; Bandel, 1975; Penchaszadeh and De Mahieu, 1975, 1976; Goodwin, 1979; Eyster, 1980; Barkati and Ahmed, 1983; see reviews by Fretter and Graham, 1962; Arnold, 1971; Arnold and Williams-Arnold, 1977; Haven, 1977; Geraerts and Joose, 1984; Hadfield and Switzer-Dunlap, 1984; Mackie, 1984; Tompa, 1984; Boletsky, 1986), and for some groups, classification schemes have been proposed based on capsule or egg mass gross morphology (Andrews, 1935; Southwood, 1956; Hurst, 1967; Bandel, 1974; Fernandez-Ovies, 1981). At the levels of ultrastructure and biochemistry, the descriptive approach has been applied to relatively few species (e.g., Flower, 1973; Price and Hunt, 1974; Goodwin, 1979; Gruber, 1982; Sullivan and Maugel, 1984; see reviews by Goudsmit, 1972; Berry, 1977; Webber, 1977; Pechenik, 1979; Fretter, 1984; Hadfield and Switzer-Dunlap, 1984; Tompa, 1984;

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Eyster, 1986). Such studies indicate that molluscan encapsulating structures, particularly those of many prosobranch gastropods, are structurally and chemically complex, reflecting the underlying complexity of the encapsulation process.

We have a general understanding of the encapsulation process in gastropods and cephalopods, and a general idea of where key events probably take place, based upon observations of spawning activity and studies of capsule wall structure, female anatomy, and histochemical staining characteristics of capsules, egg mass layers, and the female reproductive tract (Fretter, 1941; Rangarao, 1963; Tamarin and Carriker, 1967; Tompa, 1976; O'Conner, 1978; Ramasubramaniam, 1979; Gruber, 1982; Sullivan and Maugel, 1984; see reviews by Fretter and Graham, 1962; Arnold, 1971, 1984; Beeman, 1977; Webber, 1977; Gruber, 1982; Fretter, 1984; Geraerts and Joose, 1984; Hadfield and Switzer-Dunlap, 1984; Tompa, 1984; Boletsky, 1986). However, many details remain to be discovered, even for those few species that have received attention.

In addition to describing capsule and egg mass morphology, a number of workers have described egg laying behavior (e.g., Ankel, 1929; Giglioli, 1955; Arakawa, 1962; Merrill and Turner, 1963; D'Asaro, 1969; Bingham *et al*., 1973; Houbrick, 1973; Castilla and Cancino, 1976; Jeppesen, 1976; Arch and Smock, 1977; Wells and Wells, 1977; Rudolph and White, 1979; Gruber, 1982), substrate selection by ovipositing females (e.g., Chess and Rosenthal, 1971; Pollard, 1975; Pechenik, 1978; Spight, 1977; Barnet *et al*., 1980; Brenchley, 1981; Boletsky, 1986; D'Asaro, 1986), and the energy content of some gastropod egg capsules (Perron, 1981a). In the genus *Conus*, the caloric content of the egg capsules accounted for up to about 50% of the total calories devoted to reproduction (Perron, 1981a). DeFreese and Clark (1983) reported the caloric content of the egg masses of 31 opisthobranch species, although they did not determine the relative contributions of the embryos and the encapsulating structures. MacKenzie (1961) and Rey and Stoner (1984) have described the variety of organisms found associated with some gastropod encapsulating structures.

The escape of offspring from encapsulating structures has been described for a number of molluscs (e.g., Vaugn, 1953; Davis, 1961, 1967; Buckland-Nicks and Chia, 1973; Gamulin, 1973; West, 1973; Chess and Rosenthal, 1971; Pechenik, 1975; see reviews by Davis, 1981; Webber, 1977; Arnold and Williams-Arnold, 1977). Do embryos of a given species always emerge from particular regions of the capsule or egg mass? Is escape effected mechanically, or does the encapsulating structure, or a portion of it, dissolve, suggesting a chemically controlled escape mechanism? How long after deposition does escape take place? How long does it take all inmates to escape once hatching begins? These questions must continue to be addressed for more species.

More descriptive work is needed. Once the intraspecific and interspecific variability in 1) capsule size, shape, structure, and chemical composition, 2) egg laying behavior, 3) production costs, and 4) escape mechanisms has been documented for a wide range of species depositing capsules or masses into a wide range of habitats, the adaptive value of this variability may be profitably considered.

THEORETICAL APPROACH

Why are particular capsules and egg masses a certain size or a certain shape? Why do they differ in consistency, thickness, and chemical composition? What impact might such differences have on the development of enclosed embryos? Why do some capsules and masses contain more or fewer embryos than those of other species? How might encapsulation benefit a species? What selective forces might account for the evolution of encapsulating structures, and especially for the present diversity of such structures often observed even within single molluscan genera? What are the evolutionary implications of encapsulation; in particular, what further shifts in life history pattern are made possible once encapsulating structures become a part of the life history?

Such questions provide a compelling rationale for continued descriptive studies of the sort reviewed above, and also encourage an approach of thoughtful speculation (e.g., Pechenik, 1979; Perron and Corpuz, 1982; Caswell, 1981; Grant, 1983; Strathmann and Chaffee, 1984). One issue that has generated particular theoretical interest concerns the evolution of "mixed" encapsulated development in marine species. Species with mixed development develop for a relatively short time within capsules or egg masses, and subsequently for a relatively long period of time as planktonic larvae, living freely in the sea. Such life histories are especially common among the Gastropoda (Thorson, 1946; Pechenik, 1979). Mixed development can apparently lead to a life history in which a planktonic larval stage is omitted; following the evolution of an egg capsule or egg mass, encapsulated embryos can, through provision of sufficient nutrients, complete development to the crawling juvenile stage within the encapsulating structure. Yet, mixed development clearly does not represent direct selection for loss of the planktonic stage since, in species with mixed development, egg cases and egg masses do not prevent the eventual planktonic dispersal of offspring. The selective pressures responsible for the evolution of mixed life histories are unclear. What adaptive benefits of mixed development might account for its evolution? The question has generated some discussion (Pechenik, 1979; Caswell, 1981; Grant, 1983), but a completely satisfactory answer awaits further description and experimentation.

Encapsulation poses a number of problems for developing embryos, which are, to some extent, imprisoned within their egg casings. Perron and Corpuz (1982) and Strathmann and Chaffee (1984) have recently considered the theoretical difficulties embryos will have in acquiring oxygen and eliminating wastes from capsules and egg masses, and the consequent role that diffusion might play in limiting variation in egg mass morphology, size, and the number of individuals packaged within each mass or capsule.

The major value of theoretical treatments is in pointing out research areas where additional data are needed. Questions about the "why" of egg capsules and egg masses should lead to detailed determinations of capsule and egg mass properties, both physical and mechanical, and to studies of the tolerances and requirements of the embryos that develop within encapsulating structures, as discussed next.

EXPERIMENTAL APPROACH

Documenting the adaptive benefits resulting from encapsulation, the problems imposed by encapsulation, and the extent to which and the manner in which those problems are resolved, generally require an experimental approach.

Egg masses and egg capsules are often structurally and chemically complex and energetically costly, and their formation often requires highly modified female reproductive anatomy, physiology, and behavior, as discussed earlier. The survival benefits of encapsulation should therefore be considerable, but are poorly understood at present. Application of the experimental approach is essential to understanding the adaptive significance of capsules and egg masses, the selective forces responsible for the evolution of encapsulating structures, the nature of any limitations placed on the evolution of capsule structure and size, and limitations to the manner in which embryos are packaged.

There may be nutritional benefits to encapsulation, particularly among gastropods. In many marine gastropods, encapsulating structures enclose extraembryonic yolk (Todd, 1981) or nurse eggs (e.g., Thorson, 1950; Spight, 1976; Gallardo, 1979; Rivest, 1983) in addition to developing embryos. Egg masses and egg capsules can thus provide a vehicle for provisioning embryos with extraembryonic nutrition.

The capsular fluid can itself be nutritive in some species. This is clearly the case for many pulmonates (see reviews by Taylor, 1973; Raven, 1972) and apparently the case for at least some opisthobranchs and prosobranchs (Clark and Jensen, 1981; Rivest, 1981). Once mechanisms (nurse eggs, nurse yolk, or nutritive fluid) for providing extraembryonic nutrients arise, variation in the amount of such nutrients provided per embryo, and intracapsular variation in the abilities of embryos to compete for these nutrients, can provide a vehicle through which selection can occur for hatching size and stage of development at which hatching will take place (Thorson, 1950; Rivest, 1983; Gallardo, 1979; Spight, 1976).

In terrestrial and freshwater molluscs, egg capsules and egg masses may play important roles in providing embryos with calcium needed for cell adhesion, embryonic shell formation, or proper physiological functioning in the face of osmotic stress (Tompa, 1976, 1980; Taylor, 1973).

However, not all egg capsules subserve a clear nutritive role. Many species can be successfully reared after artificial removal from egg capsules (e.g., Costello and Henley, 1971; Lord, 1986), indicating that components of the intracapsular fluid are not essential for successful development in at least these species. Moreover, Perron (1981b) found that *Conus pennaceus* embryos developing within their egg capsules and those developing after premature removal from their egg capsules grew at comparable rates, again minimizing the nutritive role of the intracapsular fluid. Similarly, data on the size and weight distribution of encapsulated embryos of *Nucella* (= *Thais*) *lapillus* also argue against a substantive nutritional role for the intracapsular fluid in this species; on average, individual biomass declined during intracapsular development, a result consistent with continued metabolism in the absence of an external nutritive source (Pechenik *et al.*, 1984). Hoagland (1986) reports that embryos of *C. fornicata* died within two days of removal from their egg capsules, but the results may reflect exposure of the excapsulated embryos to bacterial attack rather than their removal from a nutritive source, as discussed below. Additional studies on the embryonic requirements of *C. fornicata* should be conducted.

Encapsulating structures are often said to be "protective," although few workers have determined the stresses, if any, that are effectively protected against. Capsular fluid of the few gastropod species tested does not suppress bacterial growth (Rivest, 1981; Pechenik *et al.*, 1984), but the capsular fluid of at least some species appears to be axenic (Lord, 1986). As long as bacteria cannot penetrate the intact egg capsule or egg mass of these species, encapsulation may protect developing embryos from bacterial attack; the embryos of *Nucella* (= *Thais*) *lapillus* do not long survive excapsulation (Pechenik *et al.*, 1984) except in the presence of antibiotics (Lord, 1986), demonstrating the susceptibility of early embryos to bacterial attack and indicating a protective role for the egg capsules of this species.

The ability of capsules to protect against predation has been specifically considered in only a few studies. In particular, Brenchley (1982) found that up to 52% of the egg capsules of the mud snail, *Ilyanassa obsoleta*, were preyed upon by gastropods and crustaceans. Up to 42% of *Eupleura caudata* egg capsules deposited in the field were found damaged, most likely through predation by a variety of polychaetes, gastropods, and crustaceans (MacKenzie, 1961). Similarly, *Ilyanassa obsoleta* is an effective predator upon the egg cases of *Cerithidea californica* (Race, 1982). Anecdotal information from many other sources clearly indicates that substantial predation upon egg capsules and egg masses does occur (reviewed by Spight, 1977; Pechenik, 1979). Even so, predation upon encapsulated embryos might be less than that upon free-living, planktonic embryos, so that encapsulation may offer at least relative protection from predation. Some molluscan encapsulating structures may deter predation more effectively than others, although variability in capsule or egg mass resistance to predation has never been specifically examined. Perron (1981a) reported a positive correlation between the duration of the encapsulated period of development and the resistance of *Conus* spp. egg capsules to being artifically punctured. This result indicates that embryos with longer periods of encapsulated development are placed into sturdier capsules, and suggests that these capsules may indeed be more resistant to at least some types of predators.

Pechenik (1979) suggested that, in mixed life histories, egg capsules and egg masses might be beneficial in confining embryos until they become capable of swimming up into the water, away from the threat of ingestion by benthic suspension feeders and deposit feeders. He noted that such temporary confinement would be beneficial only if predation rates in the plankton were lower than those in or near the benthos, and that the benefit would be magnified if later developmental stages were less vulnerable than earlier ones. There are still no data dealing with the first issue, but recent experiments using polychaete and sand dollar larvae clearly indicate a reduction in vulnerability to at least some predators with increasing stage of larval development (Pennington and Chia, 1984; Rumrill *et al.*, 1985). These studies of stage-dependent vulnerability to predators should be extended to include molluscan species that begin development within egg capsules or egg masses.

Few studies concern the ability of molluscan encapsulating structures to protect developing embryos from physical stress. This question is particularly relevant for species depositing egg capsules or egg masses intertidally, because the encapsulated embryos of such species will be potentially subjected to desiccation, osmotic stress, thermal stress, waste build-up, and perhaps gas exchange difficulties. The limited data presently available indicate that intertidal gastropod egg capsules do not offer much protection against water loss (Carmicheal and Rivers, 1932; Chernin and Adler, 1967; Bayne, 1968, 1969; Feare, 1970; Spight, 1977; Pechenik, 1978). The level of protection obtained seems to depend mainly on the microenvironment into which the capsules are deposited (Spight, 1977; Pechenik, 1978; Gallardo, 1979), although differences in capsule wall stiffness may also play some role in determining resistance to water loss (Daniel and Pechenik, unpublished—summarized by Feder *et al.*, 1982). More studies are needed of 1) site selection behavior by ovipositing adults, similar to those of Pechenik (1978), Brenchley (1981), and Barnet *et al.* (1980), 2) levels of thermal, desiccation, and osmotic stress actually experienced by encapsulated embryos in the field, 3) embryonic tolerance to specific levels of physical stress, and 4) functional properties of the encapsulating materials.

The cause of embryonic death under desiccating conditions has never been investigated. Evaporation from capsular fluid will elevate intracapsular osmotic concentration, so that mortality may result from high salinity stress rather than from actual drying out. Alternatively, embryos may simply be crushed as the capsules deform. It should be possible to distinguish among these possibilities through experimentation.

The egg cases of at least some intertidal prosobranch gastropod species are highly effective in protecting enclosed embryos from low-salinity stress of the sort encountered during a rainstorm at low tide, and the characteristics of the egg cases and embryos accounting for this protection have been examined. Excapsulated embryos (those which have been artificially removed from capsules) are far more vulnerable to abrupt declines in external osmotic concentration than are encapsulated embryos of the same species (Pechenik, 1982, 1983). Nevertheless, the capsule walls of the three species examined are highly permeable to water and salts; the capsules apparently protect embryos not by being impermeable and preventing exposure to lowered salinity, but by reducing the rate at which the salinity declines and, possibly, by maintaining an intracapsular osmotic concentration slightly above that of the surroundings. A comparison of these and similar data for other intertidal species with comparable data for subtidal species might reveal the extent to which intertidal capsules are specifically adapted for protection from low salinity stress. The intertidal capsules of *Ilyanassa obsoleta* are no more effective in reducing rates of intracapsular water loss under desiccating conditions than are the morphologically similar capsules of the subtidal species, *Nassarius trivittatus* (Pechenik, 1978). No other comparisons have been reported.

The susceptibility of molluscan embryos to water-soluble pollutants and the extent to which encapsulation protects these embryos from exposure to such pollutants have been little studied. Encapsulated embryos of the gastropod *Ilyanassa obsoleta* developed more slowly in the presence of 1.0 ppm No. 2 fuel oil (water accommodated fraction) relative to control embryos developing in unadulterated seawater (Pechenik and Miller, 1983), but whether this reduction in developmental rate reflects diffusion of fuel oil hydrocarbons across the egg capsule wall or simply reflects a coating effect of the oil on the outside of the capsule, limiting oxygen diffusion, was not determined. Direct measurements of capsule wall and egg mass permeability to a wide range of organic and inorganic molecules differing in size and charge would enable us to predict which pollutants might penetrate the walls of particular encapsulating structures and which pollutants might be excluded.

Although we have only limited data on the permeability of egg capsule walls to water and small molecules (Pechenik, 1982, 1983; Taylor, 1973; Raven, 1972), we know even less about permeability to dissolved oxygen. Gelatinous egg masses may pose particularly great diffusion problems for developing embryos, since the jelly represents an unstirrable barrier between the embryos and the surrounding seawater (Strathmann and Chaffee, 1984). Chaffee and Strathmann (1984) have shown that embryos of the opisthobranch *Melanochlamys diomedea* develop more rapidly near the periphery of their globular, gelatinous egg masses than those more deeply embedded within the mass; experimental manipulations strongly suggest that the asynchrony in developmental rates within a single egg mass is caused by gas (and possibly waste) diffusion problems. A species with thin, ribbon shaped egg masses, *Haminoea vesicula*, does not show such asynchronous development probably because the relatively great surface area of the ribbon-shaped mass minimizes the diffusion problem (Chaffee and Strathmann, 1984). Developing embryos of the cephalopod *Sepia officinalis* obtain oxygen by diffusion through an outer egg shell but the oxygen concentration of the perivitelline fluid surrounding the embryo is always significantly below that of the seawater surrounding the egg case (Wolf *et al.*, 1985), suggesting that the egg shell limits oxygen availability to the embryos. In this species, the egg shell becomes thinner as development proceeds, imposing less of a barrier to diffusion as the oxygen requirements of the embryo increase (Wolf *et al.*, 1985).

Another problem that would benefit from more attention from experimentalists concerns the manner in which embryos escape from egg masses and egg capsules. The hatching process of cephalopods has been clearly shown to be chemically mediated (Marthy *et al.*, 1976; see reviews by Arnold, 1971; Davis, 1981; Boletsky, 1986). In contrast to what is known about the hatching mechanism of cephalopods, the mechanisms of embryonic escape are unexplored for bivalves and chitons, and studies on gastropods are rare. Experiments on the hatching process can, however, be conducted inexpensively and without sophisticated equipment.

The basic question of whether escape is physically or chemically mediated can be approached very simply, as described for the prosobranch gastropods *Ilyanassa* (= *Nassarius*) *obsoleta* and *Nassarius trivittatus* by Pechenik (1975). Both species escape from their egg capsules in the veliger stage of development, leaving through an opening at the top of the capsule. Prior to escape, this opening is occluded by a thick plug, which Sullivan and Maugel (1984) have shown to be continuous with the two inner layers of the egg capsule wall. In the basic experiment to determine the hatching mechanism, intact egg capsule plugs were removed from freshly deposited egg capsules and sliced in half. One half of each capsule plug was placed in about 10 μl of seawater (control), and the other half was placed in about 10 μl of seawater into which veligers had recently escaped. Control plugs remained intact, whereas the other plugs soon lost their integrity. Using this simple assay, I was able to determine that plug removal is chemically mediated in *I. obsoleta* and *N. trivittatus*, that the hatching substance is species specific in action, that the substance is released by individual veligers for only a few hours, and that a single individual should be able to produce sufficient hatching substance to dislodge the plug from the top of the capsule, so that a coordinated release of hatching substance by all inmates within a capsule need not be postulated. This prediction has been corroborated by Sullivan and Bonar (1984), who observed successful hatching from an egg capsule of *I. obsoleta* containing a single veliger.

Sullivan and Bonar (1984) have gone on to document the biochemical characteristics and functional properties of the hatching substance produced by *I. obsoleta* in relation to capsule chemical composition. The isolated, active substance is proteinaceous (and probably an enzyme), shows peak activity at 20°C, is inactivated somewhere between 40 and 50°C, and can function at temperatures at least as low as 0°C. Veligers of *N. trivittatus* successfully escape from capsules at 3°C, indicating that the hatching substance produced by this species also remains functional at low temperatures (Pechenik, 1978). Studies on *Nucella lapillus, Urosalpinx cinerea, Tegula pfeifferi,* and *Adelomelon brasiliana* suggest that escape is also chemically mediated in these gastropod species (Ankel, 1937; Kostitzine, 1940; Hancock, 1956; Haino, 1971; De Mahieu *et al.*, 1974). The hatching process has been described for some other molluscan species (papers cited earlier), but has not yet been explored through experimentation.

The production and secretion of species-specific hatching chemicals gives rise to some intriguing questions. For example, the evolution of the ability to manufacture egg capsules or egg masses cannot precede the evolution of the ability to escape from such structures. And yet, how can a specialized means of escape evolve before there is something to escape from? Collecting additional data on the structure, biochemistry, and details of the hatching mechanism for a variety of species in different groups should eventually permit cogent speculation on the evolution of escape mechanisms.

SUMMARY

Further experimentation on egg mass and capsule properties and on embryonic tolerances, requirements, and escape mechanisms, are essential to understanding egg capsule and egg mass functions, the vehicles through which selection for particular adaptive benefits can come about, and the extent to which physical requirements and material properties impose constraints on egg mass or egg capsule size, configuration, and structure and on the number of embryos that can be packaged into a given mass or capsule. Clarifying the evolutionary history of encapsulated development, discerning the ecological pressures selecting for this history, and predicting the future direction of reproductive pattern evolution in particular groups of molluscs will require further description, experimentation, and cautious arm waving, and will be facilitated by increased communication among the adherents of the descriptive, theoretical, and experimental approaches.

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POSTSCRIPT

Note added in proof. One additional, especially relevant paper has appeared since completion of this review:

Hunter, T. and S. Vogel. 1986. Spinning embryos enhance diffusion through gelatinous egg masses. *Journal of Experimental Marine Biology and Ecology* 96: 303-308.

PATTERNS OF ENCAPSULATION AND BROODING IN THE CALYPTRAEIDAE (PROSOBRANCHIA: MESOGASTROPODA)

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ABSTRACT

Calyptraeid egg capsules and the nutrition of eggs within the capsules are described. The anatomy of the female reproductive system as it relates to egg capsule formation is presented. Although the brooded capsules themselves are similar in the entire family, the intracapsular fluid may or may not be viscous. Embryonic nutrition varies; it can be via enclosed yolk, nurse eggs, or brood cannibalism, and in some species, encapsulated development is followed by a planktotrophic period. Type of nutrition does not obviously correlate with reproductive anatomy, nor does it follow a phylogenetic pattern within the family. Possible adaptive patterns and constraints on intracapsular developmental modes are discussed. The brooded capsules appear to have a protective function, and seem to be arranged to allow the embryos efficient respiratory exchange.

Mesogastropods in the family Calyptraeidae are characterized by the production of eggs in membranous sacs that are brooded for a time in the mantle cavity. Within each genus, some species produce large, yolky eggs that are retained in the brood sacs until they hatch as crawl-away young. Other species produce smaller eggs that hatch as veligers and complete development during a period of planktotrophy (Coe, 1949). Such congeners with differing reproductive strategies are often sympatric. There are also differences between species in encapsulation fluid and in mode of nutrition within the egg sac. The purpose of this paper is to describe these differences, then examine them taxonomically and zoogeographically.

Patterns in encapsulation and brooding will be examined in light of three potential classes of explanation: 1) taxonomic constraint, the lack of evolutionary potential for development of a trait within a particular lineage given present genetic make-up; 2) morphological constraint in which some traits are constrained by others, or "exaptation" (Gould and Vrba, 1982) in which traits were not originally selected for their current adaptive role; and 3) natural selection on individuals leading to adaptation to local ecological conditions.

METHODS

Data were collected on egg and brood characteristics of Calyptraeidae over the period 1972-1985. Diameters of uncleaved eggs and length of the young at release were measured by ocular micrometer at 25X. Dimensions of veligers taken include length, width excluding velum, and width of the extended velum. Numbers of eggs and hatching embryos per capsule and brood were determined by direct count or, in large egg masses, by counting the number of eggs in approximately 5 sacs and multiplying mean number per sac by the total number of sacs in the brood. When possible, data were taken on more than one population per species, and on at least 5 broods per population (usually many more).

Observations on fate of developing embryos and any nurse eggs inside the brood sacs were made with dissecting microscope, as were descriptions of the egg sacs and egg-laying process. Female behavior while brooding and at time of release of the brood were also observed, using animals attached to transparent watch glasses. To examine the interaction of mothers and their broods under stressful conditions of low food availability, 10 females with and 10 without broods were paired by size and placed individually in finger bowls with artificial sea water (Instant Ocean®), changed daily. Twenty controls were maintained in a flowing seawater table. Similarly, 10 pairs of test animals were subjected to unaerated natural seawater changed every other day, in individual finger bowls. These experiments with *Crepidula fornicata* (Linnaeus) were at 24 ± 2°C.

To test the role of the brood chamber and capsule in embryo development, 25 broods of *Crepidula fornicata* were removed from the parent and maintained in artificial seawater. Embryos were removed from one capsule of each brood and placed in artificial seawater. Five broods were removed from the parent and placed in natural seawater. All experiments were conducted at 24 ± 2°C.

The female reproductive system was studied using

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Table 1. Species and localities studied. Note: *Cr.* cf *convexa* of Florida and the Panamic Atlantic and *Cr.* cf *plana* of Florida are species being described elsewhere. The *Cr.* cf *convexa* from the two localities are different species.

SPECIES	COUNTRY	STATE OR PROVINCE	LOCALITY
Calyptraea			
conica Broderip	Panama		Noas Is.; Venado Is.
	Costa Rica	Guanacaste	Punta Morales
mamillaris Broderip	Costa Rica	Guanacaste	Isla Tolinga, Gulfo de Nicoya; Bahia Cocos (dredged)
Crepidula			
aculeata (Gmelin)	USA	Florida	Key Biscayne; Ft. Pierce
adunca Sowerby	USA	California	Monterey Peninsula
cerithicola C.B. Adams	Panama		Taboga Is.; Farallón (dredged)
convexa Say	USA	Massachusetts	Woods Hole; Martha's Vineyard;
		Conecticut	Bridgeport; Niantic
		Rhode Island	Little Compton
		New York	Oyster Bay, Long Island
cf *convexa*	USA	Florida	Gulf Breeze; Ft. Pierce
cf *convexa*	Panama		Coco Solo, Limón Bay (Atlantic side)
echinus (Broderip)	Panama		Taboga Is.; Venado Is.; Naos Is.
fornicata (Linné)	USA	Same as *C. convexa*, plus:	
		Maine	Kettle Cove
incurva (Broderip)	Panama		Naos Is.; Venado Is.
lessonii (Broderip)	Panama		Naos Is.; Venado Is.; Rio Mar
lingulata Gould	USA	California	Balboa Is.
navicula Mörch	Bahamas	Grand Bahama Is.	East end
onyx Sowerby	USA	California	Balboa Is.
plana Say	USA	Same as *C. convexa*	
cf *plana*	USA	Florida	Ft. Pierce
protea d'Orbigny	Brasil	Rio Grande	Rio Grande do Sul (dredged)
striolata Menke	Panama		Taboga Is.; Venado Is.; Naos Is.; Farfan Flats; Rio Mar
	Costa Rica	Guanacaste	Punta Morales; Bahia Cocos
Crucibulum			
personatum Keen	Costa Rica	Guanacaste	Punta Morales
	Panama		Naos Is.; Venado Is.
scutellatum Wood	Panama		Naos Is., Venado Is.
	Costa Rica	Guanacaste	Bahia Cocos (dredged)
spinosum (Sowerby)	Panama		Naos Is.; Farfan Flats; Venado Is.
	Costa Rica	Guanacaste	Bahia Cocos (dredged)
umbrella (Deshayes)	Panama		Naos Is.; Venado Is.
	Costa Rica	Guanacaste	Bahia Cocos; Punta Cacique (dredged)
Hipponix			
grayanus Menke	Costa Rica	Guanacaste	Bahia Cocos; Bahia Huevos; Bahia Culebra

standard techniques of micro-dissection on living tissue, staining living tissue with methylene blue and neutral red and finally with Bouin's solution (Davis, 1983).

Species examined include 6 species of *Crepidula* from the northwestern Atlantic, one from Brasil, one from the Bahamas, and one from the Caribbean Sea. Fourteen species of Calyptraeidae were studied in 1985 from the Pacific coasts of California, Panama and Costa Rica. Exact localities are found in Table 1. All species of Calyptraeidae and Hipponicidae collected in February-March, 1985 were found with broods. Voucher specimens of adults and broods are on deposit at the Academy of Natural Sciences of Philadelphia. Data on egg capsules of some species not personally examined were taken from the literature, as indicated by references in the text.

RESULTS

ANATOMY AND PROCESS OF ENCAPSULATION

The female reproductive system in all species examined consists of a gonad with gonopericardial duct, seminal recepticles, and a large pallial oviduct containing glandular folds, where eggs are encapsulated. Figures 1 - 3 illustrate interspecific variation within the Calyptraeidae. Most species of *Crepidula* have a well-developed pallial oviduct consisting of three parts: a posterior portion where fertilization occurs, a glandular portion where yolk is laid down, and an anterior muscular portion, narrowing to a neck and finally a genital papilla (Figs. 1,2). In *Crepidula aculeata* (Fig. 3), however, the anterior portion is absent, as it is in *Calyptraea mamillaris* Broderip from Costa Rica, and

Crepipatella lingulata Gould from Southern California.

The degree of development of the glandular region of the pallial oviduct and the number of seminal recepticles do not correlate with capsule shape, the type of eggs produced, or with the number of eggs per sac. *Crepidula incurva* (Broderip) and *C.* cf *convexa* (Fig. 2) of Caribbean Panama have planktonic and nonplanktonic development respectively, yet are antomically similar with respect to pallial oviduct and seminal recepticles. Both have a non-glandular region extending anterior to the seminal recepticles and some seminal recepticles with short stalks. The major difference is that *C. incurva* tends to have more recepticles (5-6 instead of 2-4). *Crepidula aculeata* and *C. lessonii* have a similar pattern of development, yet differ strikingly in the glandular portion of the pallial oviduct (Figs. 1, 3).

The process of encapsulation was first described by Werner (1948) for *Crepidula fornicata*. I have confirmed his observations for that species and for *Crepidula plana* Say, both of which produce numerous small eggs that complete their development in the plankton. Once fertilized and coated with yolk, the eggs travel into the muscular portion of the pallial oviduct. By this point they are grouped into sausage-shaped packets. The packets are expelled from the genital papilla and pressed to the base of the propodium (Fig. 4), then transported to the underside of the propodium in a ciliated track. When expelled, the packets are already surrounded by a thin membrane, but the origin of the capsule membrane is not known. The packets are next shaped by the propodium as it alternately contracts and stretches; at the end of this process, a stalk is drawn out from the packet membrane and the finished capsule (Fig. 5) is attached either to the hard substratum directly beneath the female, or to the propodium itself. The brood may consist of as many as 100 capsules, which fill the space between the neck lappets and propodium, and obscure the gill in ventral view (Fig. 4).

Werner (1948) believed that the muscular portion of the pallial oviduct was responsible for formation of the egg packets. However, the *Calyptraea, Crepipatella,* and *Crepidula aculeata* all lack the muscular portion and indeed, the genital papilla. Their egg capsules have the same configuration as those of the species of *Crepidula* with these anatomical characters. Therefore, the muscular portion and the genital papilla are not essential for capsule formation.

Werner (1948) noted that some gastropods have a foot

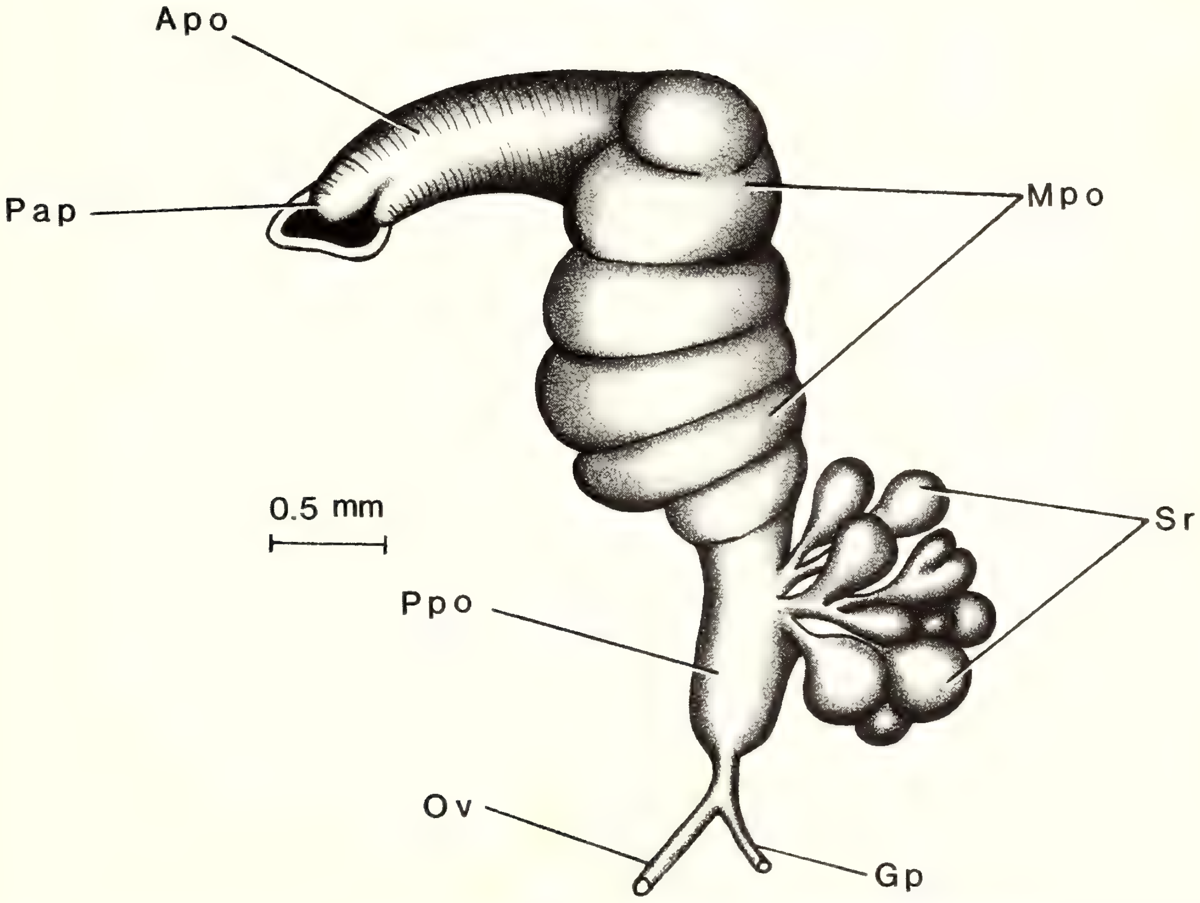

Fig. 1. Female reproductive system of *Crepidula lessonii* (Broderip) from Panama. Apo = Anterior pallial oviduct; Pap = genital papilla; Mpo = medial pallial oviduct; Ppo = posterior pallial oviduct; Sr = seminal recepticles; Gp = gono-pericardial duct; Ov = oviduct.

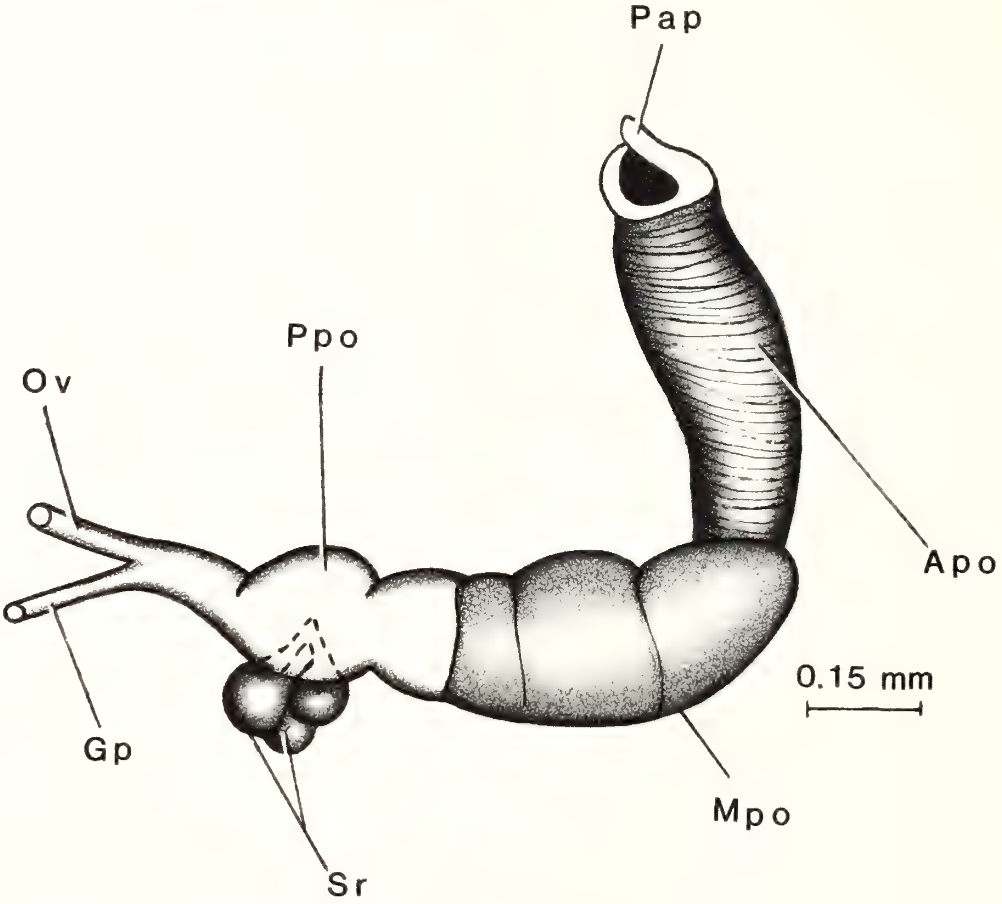
Pap
Ppo
Ov
Apo
Gp
0.15 mm
Mpo
Sr

Fig. 2. Female reproductive system of *Crepidula* cf *convexa* from Panama. Abbreviations as in Figure 1.

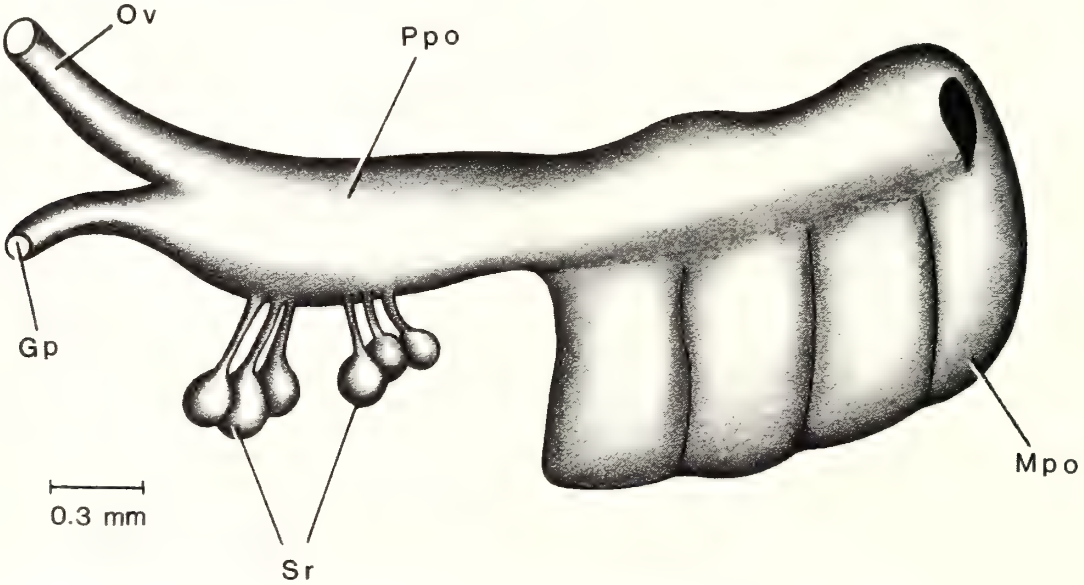
Ov
Ppo
Gp
0.3 mm
Mpo
Sr

Fig. 3. Female reproductive system of *Crepidula aculeata* (Gmelin) from Panama. Abbrevations as in Figure 1.

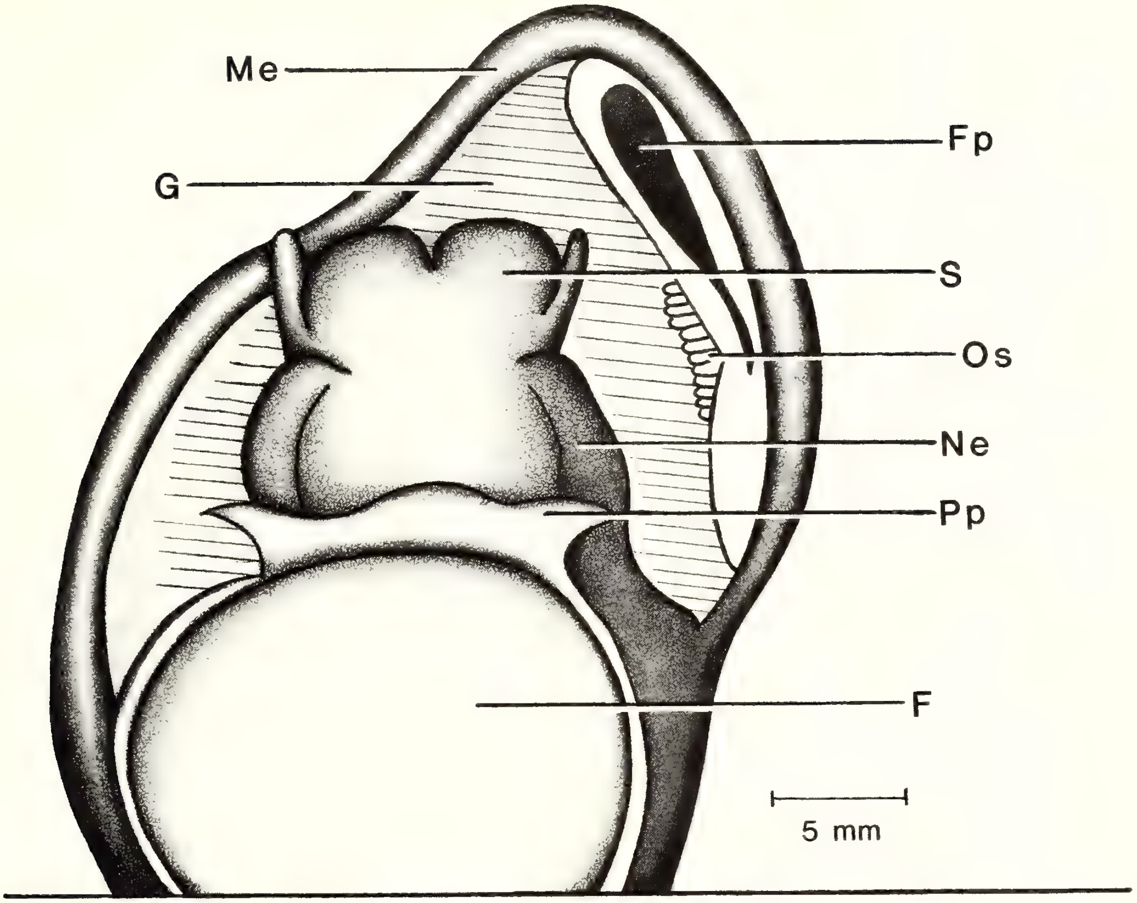

Fig. 4. Diagramatic ventral view of *Crepidula* sp. S = snout; Ne = neck lappets; G = gill; Pp = propodium; F = main part of foot; Me = mantle edge; Fp = food pouch; Os = osphradium. When laid, the egg mass is attached to the propodium or the substratum beneath it, and fills the area between the propodium and neck lappets, obscuring the gill.

gland that determines final capsule shape. Neither he nor I could detect such a gland in *Crepidula* or *Calyptraea*. Rather, the propodium seems to massage the egg packet, making the membrane of uniform thickness. The final triangular or heart-shape is mechanically the simplest possible for a stalked, non-rigid sac (Fig. 5). This shape is the same throughout the family Calyptraeidae and also occurs in the Hipponicidae.

In using *Hipponix grayanus* Menke of Costa Rica as an out-group for anatomical comparisons, I observed a major anatomical difference despite similarity in final egg capsule shape. There is a short, cupped structure on the dorsal side of the propodium to which the egg sacs are attached. This structure participates in capsule shaping and may be a foot capsule gland as sought by Werner for *Crepidula*. Histological studies are required before conclusions can be drawn.

BROODING AND RELEASE OF THE LARVAE OR JUVENILES

All species of Calyptraeidae and Hipponicidae so far examined deposit a cluster of stalked egg sacs containing one to several eggs per sac. The sac is composed of a thin membrane; the stalk is an extrusion of the membrane. The membrane appears to be double in the upper portion of the stalk. When originally deposited, the walls of the sac are flaccid and stick together. They often adhere along the midline of the sac, forcing the eggs into an arc or even two clusters within the sac. As the eggs develop, the sac becomes full and swollen. The embryos are crowded within the sac, which also contains a small amount of fluid and some cell debris and fragments of disintegrating embryos. The embryos turn about within the fluid. The proportion of embryos that do not develop varies with species. In *Crepidula fornicata*, it is about 10%, in *C. convexa* it is 23%, based on 100 broods per species examined over 3 years at Woods Hole, Massachusetts.

At release, the egg sacs split open along a cleavage line vertical along the stalk axis. There is no exit pore. All young within a capsule are necessarily released at the same time. The female raises and lowers the shell at the release of her brood, and in *C. fornicata* at least, sometimes uses the radula to pull the egg sacs free of her mantle cavity. When released, the young are either veligers, pediveligers, or crawl-

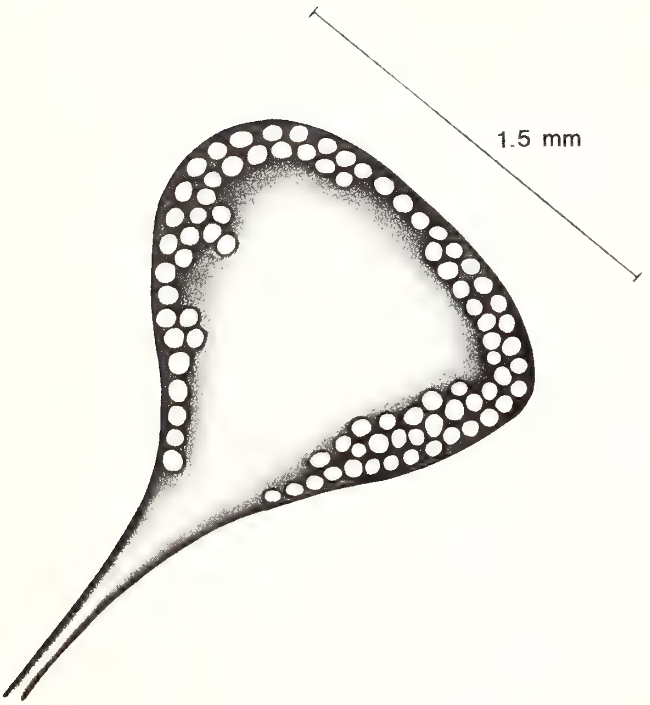

Fig. 5. Diagramatic view of a single egg capsule of a typical calyptraeid gastropod.

ing young, depending on the species. The crawling young of the Calyptraeidae have evidence of shell coiling but have lost the operculum. However, the newly-hatched crawling young of *Hipponix grayanus* of Costa Rica were observed to still have an operculum.

The capsule of *Crepidula protea* from southern Brasil differs from all others of the family. Twenty-five brooding females dredged off Barra, Rio Grande do Sul, in 25-30 m of water, were found to have embryos embedded in a gelatinous matrix in which they did not move freely (Hoagland, 1983). It is not known if the matrix has a nutritive or a protective function.

The egg capsule of calyptraeids are brooded beneath a gill enlarged for filter-feeding (Fig. 4). Therefore strong water currents carry oxygen to the permeable sacs and can remove wastes. However, the broods may interfere with respiration and/or feeding of the adult, or otherwise cause stress. To test this possibility, I examined the survivorship of females of *Crepidula fornicata* with and without broods when subjected to near starvation and to low oxygen. Survivorship under near-starvation conditions was better when larvae were not present (Table 2). Six of the 10 brooding females lifted the shell vigorously and were observed to bend the head and neck as if the broods were at the stage of hatching; the broods were expelled prematurely. Similar results were obtained when 10 pairs of test animals were subjected to unaerated seawater, except that mortality was higher in animals both with and without broods. All broods were expelled prior to death of the females (Table 2).

Survivorship of broods artificially removed from the parent and placed in aerated artificial seawater was poor. Of 25 broods of *Crepidula fornicata* removed at various stages of development, only 4 survived to hatching, and these were already at a stage possessing eye spots when removed. No broods survived when placed in natural seawater; all were consumed by ciliated protozoans. No individuals removed from the capsule survived for more than 2 days.

Table 2. Effect of starvation and low oxygen on broods and adult *Crepidula fornicata* at 24 ± 2°C.

	N	% Adult Survival at 14 days	Mean No. Days Survived	% Brood Survival	Mann-Whitney U test: probability of signif. diff.
Fed controls:					
Females	10	100	21	—	
Brooding Females	10	100	21	90	
Starved, aerated:					
Females	10	40	13.8	—	
Brooding Females	10	20	10.8	20	P<.02 *
Fed, unaerated:					
Females	10	10	6.5	—	
Brooding Females	10	0	4.6	0	.05<p<.10

*signif. difference

CAPSULE AND EGG SIZE AND NUMBER, AND NUTRITION OF EMBRYOS

The size of the calyptraeid egg sac, number of sacs, and number of eggs per sac are all variable within species, populations, and even within individuals. Nonetheless, there are species-level differences in these values (Table 3). Egg size is far more stable within species and can also be used as a species character. Smaller species tend to have larger, fewer, yolkier eggs and fewer egg sacs than larger species. The larger eggs hatch later in development, omitting the free-swimming veliger stage of the smaller eggs, although the embryos pass through a veliger stage in the egg capsule. The size of the egg sac is proportional to the number of eggs per sac, a factor related not only to species but to the size of the female as well. The number of eggs per sac also varies within a single brood; examples are given in Table 3. Control of the packaging of eggs into capsules is probably related to rate of release from the gonad and passage through the posterior pallial oviduct. No data are available to check this assumption.

The average number of young released from a brood is often substantially lower than the number of eggs laid per brood. Observations on the three North Atlantic species of *Crepidula* revealed that damaged embryos or those with abnormal development were ingested by the healthy embryos

(Hoagland, 1979). Embryos without obvious abnormality were not attacked. Cells from disintegrating embryos were swept into the gullet by means of the constantly-moving cilia of the velum. Contact between normal and disintegrating embryos appeared fortuitous, but once made, the two usually remained adpressed while cells flowed from the one to the other. This limited form of brood cannibalism began as soon as the gullet and cilia were formed. An examination of hundreds of field-collected brooding females of *Crepidula fornicata, C. plana,* and *C. convexa* Say from Woods Hole showed that, within a sac, either all embryos were viable, or all were dead. Embryos that fail to develop are rapidly consumed by the others, unless microorganisms proliferate and destroy all the embryos.

Table 4 summarizes the various types of egg development within calyptraeid egg capsules. Some species have extended the habit of brood cannibalism. In *Crepidula cerithicola*, all eggs are originally small and appear similar. They look like eggs that will become planktotrophic veligers. Some, however, develop at the expense of others. When ready to hatch, all but a few nurse eggs in each sac have been devoured. Many of the nurse eggs do divide, but at a much slower rate than the developing embryos. The embryos hatch as crawl-away young at different sizes, depending on the number of nurse eggs consumed. About 5-15 of the original 200 ± 20 per sac develop. Even more extreme is *Crepidula monoxyla* (Lesson) from New Zeland in which only 1-2 embryos per sac develop (Pilkington, 1974).

Brood cannibalism occurs both in species with small eggs destined to become planktotrophic veligers and in species with large eggs that hatch as crawling young. Although most large, yolky eggs hatch as crawling young, at least one species releases pediveligers capable of weak swimming as well as crawling (Table 4). The velum of the veliger-stage encapsulated larva beats actively and causes the larva to tumble within the capsule. It is clearly a feeding organ that continues this function in the free-living pediveliger stage.

For most Calyptraeidae, larvae develop synchronously, except for those with nurse eggs (Table 4). In only one species, *Crucibulum spinosum* of Panama, have I found asynchrony between sacs implying that the brood does not hatch all at once.

Although newly-hatched young of the direct-development (crawl-away) type feed with the radula rather than the gill or velum, they make no attempt to consume the gossamer egg capsule material, which is cast out or floats out of the female's mantle cavity. The stalks of the capsules often remain bundled together, but the cluster becomes torn into fragments as the embryos crawl away.

DISCUSSION

The taxonomic assignment of species in this paper is an advance over that presented earlier (Hoagland, 1977). Progress in systematics of the genus *Crepidula* has come through study of egg capsules and larval development coupled with electrophoresis (Hoagland, 1984) and anatomy. The species *Crepidula cerithicola* had been synonymized with *C. onyx*, but is a valid species with nurse eggs rather than planktotrophic development. Study of specimens formerly assigned to *Crepidula convexa* has proven them to be distinct species in the Panamanian Caribbean region, Florida, and the Bahamas. The name *C. navicula* is available for the northern Caribbean specimens. *Crepidula plana* in the Atlantic is two species; the southern U.S. species lacks planktotrophic development. Finally, *Crepidula echinus* must be taken out of synonymy with *C. aculeata*; it has a veliger stage and differs from *C. aculeata* in shell sculpture and anatomy. These and other changes will be reviewed in a paper devoted to systematics of the genus *Crepidula*.

Calyptraeid egg capsules are very similar to one another in construction, despite anatomical differences in the female reproduction system and differences in intracapsular fluid and nutrition. The developing embryos of calyptraeids are well-oxygenated by virtue of the shape and permeability of the egg capsules, and the presence of fluid that allows movement of the embryos within. The location of the capsule cluster under the gill where waters currents are strong aids in respiratory exchange. Division of the brood into numerous sacs may also aid in oxygenation, as well as limit losses due to predatory microorganisms.

Chaffee and Strathmann (1984) pointed out that thin-walled capsules with internal circulating fluid are more efficient than gelatinous capsules in providing oxygen to embryos; this type of capsule favors synchronous development of embryos, as found in most Calyptraeidae (Table 4). The gelatinous capsule material of *Crepidula protea* would suggest lower diffusion of oxygen and slower development than the other species. However, those capsules examined appeared to be developing synchronously.

The experiments on brood and adult survival under low food and oxygen imply that brooding does have costs to the female beyond that of capsular materials, as had been suggested by preliminary experiments (Hoagland, 1979). Brooding may interfere with respiration and/or feeding. Release of broods prematurely by stressed adults could be a means of improving adult survivorship, but at least in the non-recirculating water of containers used in these experiments, adults that released their broods also died. Larvae removed from the protection of the brood chamber were subject to attack by ciliated protozoans and bacteria. Calyptraeid egg capsules do not themselves play a protective role, but encapsulation within the brood chamber reduces mortality, and could be the selective advantage maintaining a period of brooding in all species of the family (Pechenik, 1979). Most freely-deposited molluscan egg capsules are much tougher and appear less permeable than calyptraeid capsules (Perron and Corpuz, 1982).

Although there is a dichotomy of egg size in the Calyptraeidae based on mode of reproduction, it is not clearly bimodal as one might expect (Table 3). The reason is the presence of nurse eggs (e.g. *C. philippiana*) and significant brood cannibalism (e.g. *C. convexa*) in some species. The percent variation in egg size for a given species is much smaller than the variation in capsule size, egg number, or

Table 3. Quantitative brood characteristics for Calyptraeidae and one Hipponicidae used as the out-group comparison. Data from the literature are referenced below. L = length; W = width; D = diameter; V = veliger; C = crawling young; PV = pediveliger; - = no data. Mean values and (range) for the species, where data are available. Veliger size range given as length.

Taxon	Female L	Egg D (μ)	Embryos per sac	Sacs per Brood	Hatching Stage	Hatching L (μ) (For Veligers, LxWxVelum L)	Nurse eggs/ Sac
Calyptraeidae							
Calyptraea							
conica	30 (24-33)	200 —	137 (50-200)	20 (13-33)	V	360x240x- (320-380)	—
mamillaris	16 (11-20)	200 —	80 (50-160)	16 (14-19)	V	360x240x400 (320-380)	0
novazelandiae[a]	—	—	— (4-15)	—	C	— (1050-1130)	(numerous)
Crepidula							
aculeata	18 (14-25)	380 (360-390)	19 (6-35)	11 (8-14)	C	840	0
adunca[b]	21 —	410 (400-420)	18 (15-25)	10 (8-12)	C	—	0
cerithicola	19 (12-27)	170 (160-180)	9 (5-14)	25 (11-41)	C	800 (670-920)	185 (105-300)
convexa	13 (11-17)	300 (280-320)	10 (4-18)	18 (11-25)	C	1000 (900-1080)	0
cf *convexa* (Florida)	12 (9-24)	~300 —	8 (5-16)	15 (6-27)	PV	840 —	0
cf *convexa* (Panama)	6.4 (5-8)	300 (260-400)	3 (1-5)	11 (7-16)	C	800	1 (1-2)
dilatata[c]	35 (20-50)	~238 (195-263)	22 (18-24)	21 (12-30)	C	— (900-1370)	343 (308-369)
echinus	25 (22-30)	180 —	300 (210-380)	21 (17-30)	V	360x240x420	0
fecunda[c]	51 (34-65)	212 (204-238)	600 (200-1200)	50 (30-75)	V	— (500-560)	0
fornicata	38 (15-55)	170 (160-180)	160 (80-300)	43 (25-75)	V	— —	0
incurva	13 (10-19)	160 —	52 (20-150)	43 (15-70)	V	200x250x240	0
lessonii	21 (18-30)	260 —	71 (31-80)	48 (28-70)	V	320x200x360	0
lingulata	15 (9-18)	150 —	200 (10-400)[b]	12 (7-20)[b]	V	—	0
maculosa[d]	~18 —	440 —	— (8-10)	— (10-12)	C	—	—
monoxyla[a]	— —	— —	1 —	— —	C —	— (2500-3250)	>100
navicula	— —	— —	8 (4-12)	16 (10-20)	C	—	0
onyx	33 (21-50)	172 (160-180)	220 (100-300)	49 (19-60)	V	—	6 (malformed)
philippiana[e]	— (16-29)	150 (140-160)	1 —	— (15-74)	C	3000 —	~300 —
plana	25 (14-47)	136 (130-140)	130 (40-180)	31 (19-50)	V	—	0
cf *plana* (Florida)	20 (12-27)	— —	7 (5-9)	22 (12-28)	C	900 —	0
protea	10 (7-15)	~150 —	61 (33-120)	32 (17-48)	V	—	0
striolata	16 (13-29)	160 (140-180)	63 (34-70)	43 (24-55)	V	400x280x400 (240-440)	0

continued

Table 3. Continued.

Taxon	Female L	Egg D (μ)	Embryos per sac	Sacs per Brood	Hatching Stage	Hatching L (μ) (For Veligers, LwXxVelum L)	Nurse eggs/ Sac
Crucibulum							
marense[f]	24	—	—	—	C	—	0
	—		(13-16)	(11-17)		(1020-1160)	
personatum	28	—	275	30	V	320x240x360	0
	—		(250-300)	—		—	
scutellatum	30	—	200	20	V	—	0
	—		—	—			
spinosum	19	—	200	20	V	280x240x320	0
	(12-36)		(100-300)	(13-35)		(240-360)	
umbrella	30	—	150	31	V	440x280x600	0
	—		(100-220)	(15-41)		(380-480)	
Hipponix							
grayanus	11	—	16	7	C	—	0
			(12-20)	—			

[a]Pilkington, 1974; [b]Coe, 1949; [c]Gallardo, 1977b; [d]Hoagland and Coe, 1982; [e]Gallardo, 1977a; [f]Penchaszadeh, 1985.

Table 4. Types of egg development and nutrition within egg capsules of Calyptraeidae.

Egg Type	Hatching Stage	Development Rate	Example
Small eggs	Planktotrophic veliger	Synchronous	*C. fornicata*
		Asynchronous by sac	*C. spinosum*
		Asynchronous within sac	*Calyptraea conica*
Small eggs with nurse eggs	Crawling young; feed with radula	Asynchronous within sac	*C. cerithicola*
Large lecithotrophic eggs	Pediveligers; feed with velum	Synchronous	*C.* cf. *convexa* Florida
	Crawling young; feed with radula	Synchronous	*C. convexa*
	Crawling young; brood cannibalism extensive	Asynchronous within sac	*C.* cf. *convexa* Caribbean Panama

capsule number, all of which increase with female size (Table 3; see also Gallardo, 1977b). Intraspecific variability in size of the juveniles at hatching depends on the extent of brood cannibalism or the production of nurse eggs. These two forms of nutrition are not clearly distinct in the Calyptraeidae because nurse "eggs" do begin to divide. All species examined to date have the potential to feed on siblings within the brood sac if they are damaged artificially (Hoagland, 1979). The developmental stage at hatching is, however, genetically determined and fixed for each species of Calyptraeidae (Hoagland, 1977; 1984). It is not related to the amount of food available within the brood capsule.

Rivest (1983) reported that the ratio of nurse eggs to embryos is genetically determined in *Searlesia dira* (Reeve). That ratio appears to be distinct for particular calyptraeids also (Table 3). Nurse egg production could have evolved because it is a genetically simpler path to increased hatchling size than is direct increase in egg size. Larger egg size could lower the development rate (Spight, 1975). The advantages of larger hatchling size are reduced predation and faster growth upon hatching (Rivest, 1983).

Species with and without a planktonic larval stage occur in each genus of Calyptraeidae and Hipponicidae (Table 3). We have direct fossil evidence that *Crepidula* has brooded egg capsules at least since the early Pliocene (D.R. Lindberg, pers. comm.). Non-planktonic development must have evolved many times, independently, if indeed we can make the assumption that planktonic development is primitive within the family. Since the capacity of brood cannibalism and nurse egg nutrition is widespread in calyptraeids due in part to the encapsulation process, and the basic embryology of the female reproductive system is the same in both planktotrophic and non-planktotrophic species, one might expect it to be possible to find the two modes of development in a single species. Valentine and Jablonski (1982) theorize a shifting proportion of genotypes with longer or shorter larval lives based on local selection pressure within a species as a means to evolve different modes of reproduction. However, I have never found two hatching stages in a single species of Calyptraeidae, much less in a single population (Hoagland, 1984). Evolutionary shift from one type of reproduction to another must occur rapidly, yet probably is not based on one or a few genes, or it would occur frequently at the population level. One must postulate strong selection pressure within populations acting on reproduction and/or strong reproductive isolation and divergence of other characters once a change in mode of reproduction occurs.

Zoogeographical comparison of nutritional types (Table 5) reveals that calyptraeid species thus far reported to have small non-yolky nurse eggs all occur in the Pacific Ocean. The *Crepidula* cf *convexa* from the Atlantic side of Panama (Table 3) has extensive brood cannibalism, but more embryos develop than not and the uncleaved eggs are large and yolky. Non-planktonic developers are relatively more common in the Caribbean, while planktotrophy is more common in the Panamic Province where upwelling occurs.

Both planktotrophic development and brooded development occur in species living sympatrically (Hoagland, 1977; 1979; 1984). Therefore, the advantage of one or the other reproductive mode is not related to a particular environment. For example, in Florida, *Crepidula aculeata* has non-planktonic development; it lives together with the planktotrophic *C. plana* on the same shells. Likewise, the species referable to *C.* cf *plana* in Florida has completely brooded development and lives microsympatrically with *C.* cf *convexa* that releases pediveligers.

Do patterns of egg and egg capsule morphology in Calyptraeidae fit evolutionary models of adaptation or constraint? All species copulate and none have lost the early brooding stage within multiple thin-walled egg capsules. This pattern could be considered phylogenetic background, although it could also be considered an adaptive peak, because the resulting lower early mortality has adaptive significance. Certainly capsular shape and form are co-adapted with the physical configuration and chemical environment of the brood chamber. But at least one species, *Crepidula protea*, has altered the intracapsular fluid making it viscous, and other changes are possible in this otherwise highly co-adapted set of characters. Phylogenetic constraint is not an explanation for nurse egg production or planktotrophy, for these patterns are polyphyletic.

Morphological constraint is a possible explanation for reproductive patterns. It may be that small species are constrained by available energy. They cannot produce enough eggs of the size necessary to develop to the veliger stage in the brood capsules, that will then survive the rigors of planktotrophic development at a rate great enough to replace the adult population. Hence they must switch to fewer, larger, well-protected non-planktonic eggs with a high probability of survival. Efficient reproduction can also be accomplished with nurse eggs or brood cannibalism. Data addressing this hypothesis will be presented in another paper.

Table 5. Zoogeography of some American Calyptraeidae: Number of species of each development type in each region.

	ATLANTIC		PACIFIC	
	Northwest Atlantic	Florida, Caribbean	California	Central America
Direct development	1	5	4	0
Pediveliger	0	1	0	0
Nurse eggs*	0	0	0	2
Planktotrophic	2	3	6	11

* Also known for 2 Chilean and 1 New Zealand species.

It is clear from Table 3 that small species do tend to be direct-developers, but there are some exceptions in the Pacific upwelling region. Adaptation must be considered. Perhaps in the upwelling region, the greater year-round availability of food energy to filter-feeders and cooler summer water temperature allows relaxation of the energetic/morphological constraints imposed by small size.

The presence of more direct-developing species of Calyptraeidae in the Caribbean relative to the Pacific Panamic region could have at least one other explanation. The Caribbean has highly disjunct suitable habitat (hard substratum such as cobbles or shells) separated by expanses of sand. The Panamic Pacific tends to have long stretches of cobble and rock shores. The disjunct habitat in the Caribbean could select for nonplanktonic development much as islands select for flightless birds. Allopatric speciation of non-planktonic species clearly has occurred; the distributional ranges of species that brood the young to the crawling stage are much smaller than those of planktonic species (Hoagland, 1977).

In summary, the observed patterns of egg development in the Calyptraeidae have some basis in phylogenetic constraints, broadly interpreted, but intrageneric variation could be due to a combination of size constraint and direct adaptation. The capsules of calyptraeids are protective only in conjunction with brooded development. They appear to be adapted for efficient gas exchange and rapid, synchronous larval development. The cost to females associated with brooding includes loss of respiratory and feeding efficiency.

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LABORATORY SPAWNING, EGG MEMBRANES, AND EGG CAPSULES OF 14 SMALL MARINE PROSOBRANCHS FROM FLORIDA AND BIMINI, BAHAMAS

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ABSTRACT

Specific substrata or locations used for oviposition and external and internal structure of egg capsules produced by small prosobranchs from seagrass beds and coastal splash pools are described. Included are *Tricolia affinis affinis* (C.B. Adams, 1850), *T. thalassicola* Robertson, 1958, *T. bella* (M. Smith, 1937), *Puperita pupa* (Linné, 1767), *Smaragdia viridis viridemaris* Maury, 1917, *Littorina mespillum* (Mühlfeld, 1824), *Alvania auberiana* (Orbigny, 1842), *Rissoina catesbyana* (Orbigny, 1842), *R. bryerea* (Montagu, 1803), *Zebina browniana* (Orbigny, 1842), *Rissoella caribaea* Rehder, 1943, *Caecum nitidum* Stimpson, 1851, *Marginella aureocincta* Stearns, 1872, and *Granulina ovuliformis* (Orbigny, 1841).

Populations of mature adults were collected at locations in Florida and Bimini, Bahamas, acclimated in the laboratory, and allowed to spawn in polystyrene Petri dishes. Descriptions were based on egg capsules from 10 spawning events. Egg diameter ranged from 0.07 to 0.31 mm. Species with direct development had the largest egg diameters and the smallest number of ova (two or less) per capsule. Of species with capsules formed in the oviduct, seven deposited only one or two capsules per spawning event. Except for *Smaragdia viridis viridemaris,* the largest egg capsules were less than 1.0 mm in diameter. *Zebina browniana, Rissoella caribaea*, and both marginellids had direct development.

Of species with attached egg capsules, all selected specific substrata or locations for oviposition. The selections were: *Smaragdia viridis viridemaris*, flat clean substrata (seagrass leaves, culture dishes); *Puperita pupa,* holes in calcium carbonate substrata; *Alvania auberiana*, bifurcating rhodophyte thalli; *Rissoina catesbyana*, holes rasped in thalli of rhodophytes; *R. bryerea*, culture dishes, usually at one edge; *Zebina browniana*, inverted on the culture dish covers or under seagrass blades; *Rissoella caribaea,* hidden in epiphytes on rhodophyte thalli; *Marginella aureocincta*, culture dishes; and *Granulina ovuliformis*, seagrass leaves. The remaining species released free ova encased by vitelline membranes, or they released egg capsules that were planktonic (*Littorina mespillum*, and *Caecum nitidum*).

The structure of enclosing layers ranged from vitelline membranes with secondary mucoid layers (*Tricolia* spp.) to complex encapsulations with several proteinaceous layers. *Puperita pupa* and *Smaragdia viridis viridemaris* had typical neritacean egg capsules except that the latter did not add mineral particles to exposed capsular surfaces. *Littorina mespillum* had planktonic egg capsules like those produced by most littorinaceans. *Rissoina catesbyana, R. bryerea,* and *Zebina browniana* had capsules covered by a matrix. Their capsules were specially structured so that placement in holes or crevices would not prevent hatching. *Caecum nitidum* employed the caecid method of enclosing egg capsules in feces. *Marginella aureocincta* and *Granulina ovuliformis* had inflated, plano-convex encapsulations, typical of most marginellids, that were hardened to resist predators during an extended period of development.

Reviews of molluscan biology by Morton (1967), Hyman (1967), Purchon (1968), and others have shown that encapsulation of ova is a widespread phenomenon, with the more elaborate and variable examples occurring in Prosobranchia. Adaptive advantages to prosobranchs are derived from protection and accumulation of nutritional resources (Purchon, 1968). In species which deposit ova in capsules, delicate embryonic and early larval stages are not required to face as wide a spectrum of predators as do offspring of more primitive spawners that broadcast unprotected ova. Encapsulation usually provides greater room for development than the oviducal lumen; therefore, proportionally more progeny can develop further or even become juveniles, before being released. Prosobranch egg capsules are frequently highly refractory proteinaceous envelopes (*Busycon carica* [Gmelin, 1791); Goldsmith *et al.*, 1978) that may be second-

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arily armored with environmental debris or sand (*Epitonium albidum* [Orbigny, 1842]; Robertson, 1983). Capsules can be placed on specific types of substrata (*Calotrophon ostrearum* [Conrad, 1846]; D'Asaro, 1986), deposited in locations that provide camouflage (*Assiminea californica* [Tryon, 1865]; Fowler, 1980), or positioned beyond the reach of many predators (intertidal capsules of some neritids; Andrews, 1935). Placement can also be in an environment with an assured food-supply for hatchlings (some muricids on barnacles) or can even contribute to distribution of the species (planktonic egg capsules of littorinids; Bandel, 1974). Encapsulation permits access to secondary supplies of food from accessory glands (albumen) in addition to the primary yolk in the ovum. Even the products of ovarian vitellogenesis can be concentrated by a few encapsulated embryos, if nurse eggs are made available or if cannibalism exists (*Buccinum undatum* [Linné, 1758]; Portman, 1925).

This report addresses two aspects of encapsulation in marine Prosobranchia: (1) selection of specific substrata or locations for oviposition, and (2) external and internal capsular structure. The snails studied were collected from two ecosystems heavily impacted by human activity: shallow water seagrass beds and splash pools on coastal limestone platforms. Snails with lengths less than 1 cm were included because they are especially numerous in the selected ecosystems and because they make a significant contribution to food chains (Moore, 1963). Almost no reproductive data concerning encapsulation exist for Floridian marine tricoliids, rissoids, rissoinids, rissoellids, and caecids. Their breeding behavior can be inferred from what is known about European species, presented in reports by Fretter and Graham (1977, 1978), or limited data on Caribbean and South American species, especially as reported by Marcus and Marcus (1960, 1963), and Indo-Pacific species, as summarized by Robertson (1985).

METHODS

Populations of mature adults were collected from shallow water seagrass beds and yellow zone splash-pools on limestone platforms in Florida and Bimini, Bahamas, at the locations indicated in Table 1. Also collected were samples of specific substrata occupied by adult snails and living food-organisms.

In the laboratory, populations were initially established in 8-cm, glass culture dishes until acclimated to 22 ± 2°C. For daily observations after acclimation, subsamples were transferred to covered 5-cm polystyrene Petri dishes that had been soaked in seawater. Field salinities ranged between 34 and 41 $^0/_{00}$; therefore, seawater in the same range was used for all cultures and was changed daily. Preferred foods (Table 2) were supplied in abundance daily or as needed. All material added to culture dishes was inspected for extraneous egg capsules.

Except for the tricoliids, neritids, littorinids, and caecids, spawning adults were supplied with a choice of substrata for oviposition. Included were calcium carbonate

Table 1. Locations in Florida and the Bahamas at which adults were collected, and specific substrata on which they were found, January - May 1985.

SPECIES	LOCATION	SUBSTRATUM
Tricolia affinis affinis	South Biscayne Bay	*Thalassia testudinum* *Syringodium filiforme*
	Key Largo (Card Sound)	*Thalassia testudinum* *Laurencia obtusa*
	Lower Matecumbe Key (Whale Harbor)	*Laurencia poitei*
Tricolia thalassicola	Key Biscayne (Mashta Island)	*Halodule wrightii*
Tricolia bella	North Bimini (west side)	*Thalassia testudinum*
Puperita pupa	South Bimini (Round Rock, N. Turtle Rock)	Oolitic limestone
Smaragdia viridis viridemaris	Key Biscayne (Mashta Island)	*Halodule wrightii*
	Virginia Key (Norris Cut)	*Halodule wrightii*
Littorina mespillum	South Bimini (Round Rock, N. Turtle Rock)	Oolitic limestone
Alvania auberiana	Key Biscayne (Mashta Island)	*Laurencia obtusa*
	Virginia Key (Norris Cut)	*Halodule wrightii*
	Key Largo (Card Sound)	Rhodophytes
Rissoina catesbyana	St. Joseph Bay (West side)	*Laurencia obtusa*
Rissoina bryerea	Key Biscayne (Mashta Island)	*Halodule wrightii*
	Virginia Key (Norris Cut)	*Halodule wrightii*
	Biscayne Bay (Matheson Hammock)	*Halodule wrightii*
Zebina browniana	Key Biscayne (Mashta Island)	*Halodule wrightii*
Rissoella caribaea	South Bimini (east side)	*Amphiroa* sp., *Laurencia poitei*, rhodophytes
	Lower Matecumbe Key (Whale Harbor)	*Laurencia* sp.
	Key Biscayne (Mashta Island)	Rhodophytes
Caecum nitidum	Key Biscayne (Mashta Island)	*Halodule wrightii*
	Virginia Key (Norris Cut)	*Halodule wrightii*
Marginella aureocincta	Key Biscayne (Mashta Island)	*Halodule wrightii*
	St. Joseph Bay (west side)	*Laurencia obtusa* *Thalassia testudinum*
Granulina ovuliformis	Key Biscayne (Mashta Island)	*Halodule wrightii*
	Virginia Key (Norris Cut)	*Halodule wrightii*
	Biscayne Bay (Matheson Hammock)	*Halodule wrightii*

Table 2. Foods consumed by cultured prosobranchs.

SPECIES	FOOD
Tricolia affinis affinis *T. thalassicola* *T. bella*	Epiphytes on seagrasses and macroalgae, filamentous portions of rhodophytes.
Puperita pupa	Diatoms, filamentous chlorophytes, and fungi.
Smaragdia viridis viridemaris	Seagrasses (*Thalassia testudinum* and *Halodule wrightii*).
Littorina mespillum	Diatoms, filamentous chlorophytes, and fungi.
Alvania auberiana	Fine detrital particles, small diatoms, including colonial species.
Rissoina catesbyana	Rhodophytes, epiphytes, and detritus.
Rissoina bryerea	Rhodophytes, epiphytes, and detritus.
Zebina browniana	Rhodophytes, epiphytes, and detritus.
Rissoella caribaea	Fine detrital particles, small diatoms including colonial species and filamentous epiphytes.
Caecum nitidum	Fine detrital particles and associated flora and fauna on hard substrata.
Marginella aureocincta	Small gastropods, especially *Alvania auberiana* and *Bittium varium*.
Granulina ovuliformis	Small crustaceans, especially harpacticoid copepods, amphipods, isopods, and tanaeidaceans.

(*Halimeda* spp. skeletons or bivalve shells and shells of conspecifics), seagrass leaves (*Halodule wrightii* Ashers., 1868 or *Thalassia testudinum* [König, 1805]) including sections near apical meristems as well as those encrusted with epiphytes, and thalli of rhodophytes. Usually the algae were *Laurencia poitei* Lamouroux, 1813, or *L. obtusa* Lamouroux, 1813, common shallow water species on which adult prosobranchs were found and representative of genera frequently found with small prosobranchs, as Warmke and Almodovar (1963) reported. Substrata were presented with roughly equal areas. For most herbivorous species, the spawning substratum was their food or had food-organisms attached. For all species, the substratum with the greatest area was the polystyrene Petri dish. Each dish was filled with seawater until the surface film just touched the cover on one side to provide a site for snails that prefer to be inverted during oviposition. Nearly all species investigated were active in the culture dishes, continually inspecting available substrata and often crawling suspended from the surface film.

Descriptions of egg capsules were based on at least ten spawning events (deposition of one or more capsules). An exception, *Granulina ovuliformis* (Orbigny, 1841), only deposited eight single egg capsules. Identification and systematic terminology are essentially as presented by Abbott (1974).

Line drawings were completed from live material by employing methods suggested by D'Asaro (1986). Scanning electron micrographs were prepared for most attached egg capsules at magnifications between 50 and 260 diameters, except for those of *Marginella aureocincta* Stearns, 1872, which were photographed at 680 diameters to demonstrate minute granulation. To facilitate counting laminae, egg capsules of most species were sectioned at 8 μm, stained in eosin-Y, and partially decolorized in ethyl alcohol.

Spawners and egg capsules were cataloged and preserved in buffered, 10 $^0/_{00}$ seawater-formalin. Measurements, made with an ocular micrometer, were based on at least 10 capsules spawned by three or four individuals. The greatest linear dimension parallel to the substratum was defined as length. Widths were measured perpendicular to length and parallel to the substratum. Heights were taken perpendicular to the substratum at right angles to length. Voucher specimens of egg capsules and spawning adults were deposited in the National Museum of Natural History, Washington, D.C. Catalog numbers identifying appropriate lots are included at the beginning of each description.

RESULTS

Tricolia affinis affinis (C. B. Adams, 1950)
(USNM 836978)
T. thalassicola Robertson, 1958
(USNM 836977)
T. bella (M. Smith, 1937)
(USNM 836979)

Within 24 hours after collection, all mature female tricoliids released gametes without interrupting grazing activity. As Marcus and Marcus (1960) noted for *Tricolia affinis cruenta* Robertson, 1958, absence of males did not inhibit spawning by females. There was no suggestion of a peak spawning period during February, March, and April, 1985. Data from the literature on ova and larval ecology of *Tricolia* spp. were tabulated by Robertson (1985).

Immediately after spawning by *T. a. affinis* and *T. thalassicola*, their ova were enclosed by thin, wrinkled, and elevated membranes identified by Marcus and Marcus (1960) as the vitelline membrane. Polar bodies were visible shortly after spawning. Within a few hours, the vitelline membranes swelled slightly and became almost spherical. *Tricolia bella*, in contrast, had smooth vitelline membranes after spawning that did not swell; thus, there was essentially no difference between average egg diameter and average diameter of the

Table 3. Enumerations of capsules and embryos, egg diameters, membrane or capsular dimensions, and developmental pattern (dimensions are in mm, N = 10 unless fewer are indicated in parentheses; DD, director development; LV, lecithotrophic veliger; PV, planktotrophic veliger; ND, not determined)

Species	Egg Diameter $\bar{X}$	Eggs or Capsules/ Spawning Event $\bar{X} \pm SD$	Embryos/ Capsule $\bar{X} \pm SD$	Membrane or Capsular Dimensions			Days to Hatch to 24°C	Developmental Pattern
				Length	Width $\bar{X} \pm SD$	Height		
Tricolia affinis affinis	0.12	12 to 192	-	-	0.14	-	1	LV (?)
Tricolia thalassicola	0.11	7 to 121	-	-	0.12	-	1	LV (?)
Tricolia bella	0.13	47 ± 21(7)	-	-	0.13	-	1	LV (?)
Puperita pupa	0.13	1 to 5	15 ± 3	0.67 ± 0.08	0.42 ± 0.25	0.31 ± 0.03	>6	PV (?)
Smaragdia viridis viridemaris	0.10	4 ± 2	81 ± 8	1.29 ± 0.12	0.98 ± 0.06	0.27 ± 0.04	29	PV
Littorina mespillum	0.11	ND	1	-	0.26 ± 0.02	0.12 ± 0.01	ND	PV
Alvania auberiana	0.09	1 to 2	12 ± 2	0.43 ± 0.05	0.34 ± 0.03	0.33 ± 0.05	7	PV
Rissoina catesbyana	0.11	1 to 2	6 ± 1	0.35 ± 0.05	0.34 ± 0.04	-	>8	PV
Rissoina bryerea	0.13	1 to 2	4 to 5	0.46 ± 0.07	0.38 ± 0.08	0.23 ± 0.08	11	PV
Zebina browniana	0.22	1 to 2	1	0.58 ± 0.08	0.57 ± 0.14	0.29 ± 0.03	28	DD
Rissoella caribaea	0.14	1	2 ± 1	0.49 ± 0.12	0.33 ± 0.03	0.31 ± 0.06	18	DD
Caecum nitidum	0.07	6 to 8	1	-	0.12 (egg capsule) 0.16 (with fecal layer)	-	2 to 3	PV
Marginella aureocincta	0.24	1 to 2	1	0.99 ± 0.05	0.60 ± 0.03	0.45 ± 0.07	35	DD
Granulina ovuliformis	0.31	1 (8)	1	0.88 ± 0.08	0.50 ± 0.02	0.42 ± 0.02	>15	DD

vitelline membrane (Table 3). Both *T. a. affinis* and *T. thalassicola* released ova associated with mucus, so that each ovum was enveloped and positioned at intervals in a continuous mucous ribbon extending from the pallial cavity. The mucous ribbons were almost invisible in seawater, but could be detected by passing a probe between adjacent ova. As a feeding and slowly spawning female crawled across the substratum, the adhesive egg-ribbon accumulated on her shell or became attached to adjacent objects. Waving movements by cephalic and epipodial tentacles frequently broke the egg-ribbon and dispersed fragments. Fretter (1955) described a mucous ovarian envelope for each egg of *T. pullus* Risso, 1826 that swelled after release and observed that the glandular lips of the urogenital opening in this species appeared to provide no additional covering for the ova. Whether the accessory mucous ribbons of *T. a. affinis* and *T. thalassicola* were produced by the ovary, oviduct, or pallial region was not determined. *Tricolia bella* was not observed producing a mucous egg-ribbon. Rather its demersal ova in non-adhesive, vitelline membranes were simply dispersed by tenticular activity. Both *T. a. affinis* and *T. thalassicola* also broadcast free ova in groups often numbering more than 100, as Marcus and Marcus (1960) described for *T. a. cruenta*. These fell immediately to the bottom of the culture dish where they developed normaly if fertilized. Broadcasting responses occurred only when females of *T. a. affinis* and *T. thalassicola* were trapped in a mass of algae or otherwise prevented from moving and may not represent typical spawning behavior. Diameters of the vitelline membrane and egg diameters for each species are shown in Table 3. Egg diameters closely approximate each other, those of *T. a. cruenta* (0.12 mm, Marcus and Marcus, 1960), and except for *T. speciosa* (Mühlfeld, 1824) (see Bandel, 1982), other *Tricolia* species as tabulated by Robertson (1985).

Ova from adults taken on seagrasses or rhodophytes associated with seagrasses were pale green with black-pigmented granules at the animal pole. In *T. a. affinis* and *T. thalassicola*, the polar pigment appeared concentrated as an obvious spot or ring. In *T. bella*, polar pigment was diffuse. Later in development, polar pigment became associated with velar cells. Egg color probably reflected diet (see Robertson, 1985), because *T. a. affinis* from patch-reef habitats with dense populations of rhodophytes, especially encrusting coralline species, produced purplish-pink ova. Development of the three species studied progressed rapidly, with veligers escaping from the vitelline capsule after approximately 24 hours. Veligers all retained considerable yolk after swimming for hours (the point at which observations ceased). As Robertson (1985) suggested, these larvae may be lecithotrophic, but further observations are necessary to confirm whether or not feeding occurs.

Puperita pupa (Linné, 1767)
(USNM 836975)

Egg capsules and spawning adults were collected from yellow zone splash pools isolated from the ocean on Round Rock and North Turtle Rock, Bimini, Bahamas, between February 26 and March 6, 1985. In the pools, adults aggregated under ledges or on and under loose rocks (oolitic limestone, and *Millepora* spp. and madreporarian skeletons) and deposited almost microscopic egg capsules in those locations. Typically, capsules were hidden in holes or depressions at least deep enough for the surface of the capsule to be level with or lower than the surface of the substratum. A sample of 50 spawning sites from several rocks in one pool included only one capsule fully exposed on a flat surface. In madreporarian calyxes, a frequently selected site, two or three capsules were usually clustered together. No capsules were found on smooth or eroded conspecific shells, a common spawning site for other neritids. Selection of depressions for oviposition by other neritid species was reported by Andrews (1935). A tabulation of published data on neritid egg capsules was presented by Govindan and Natarajan (1974).

Adults spawned in the laboratory after less than

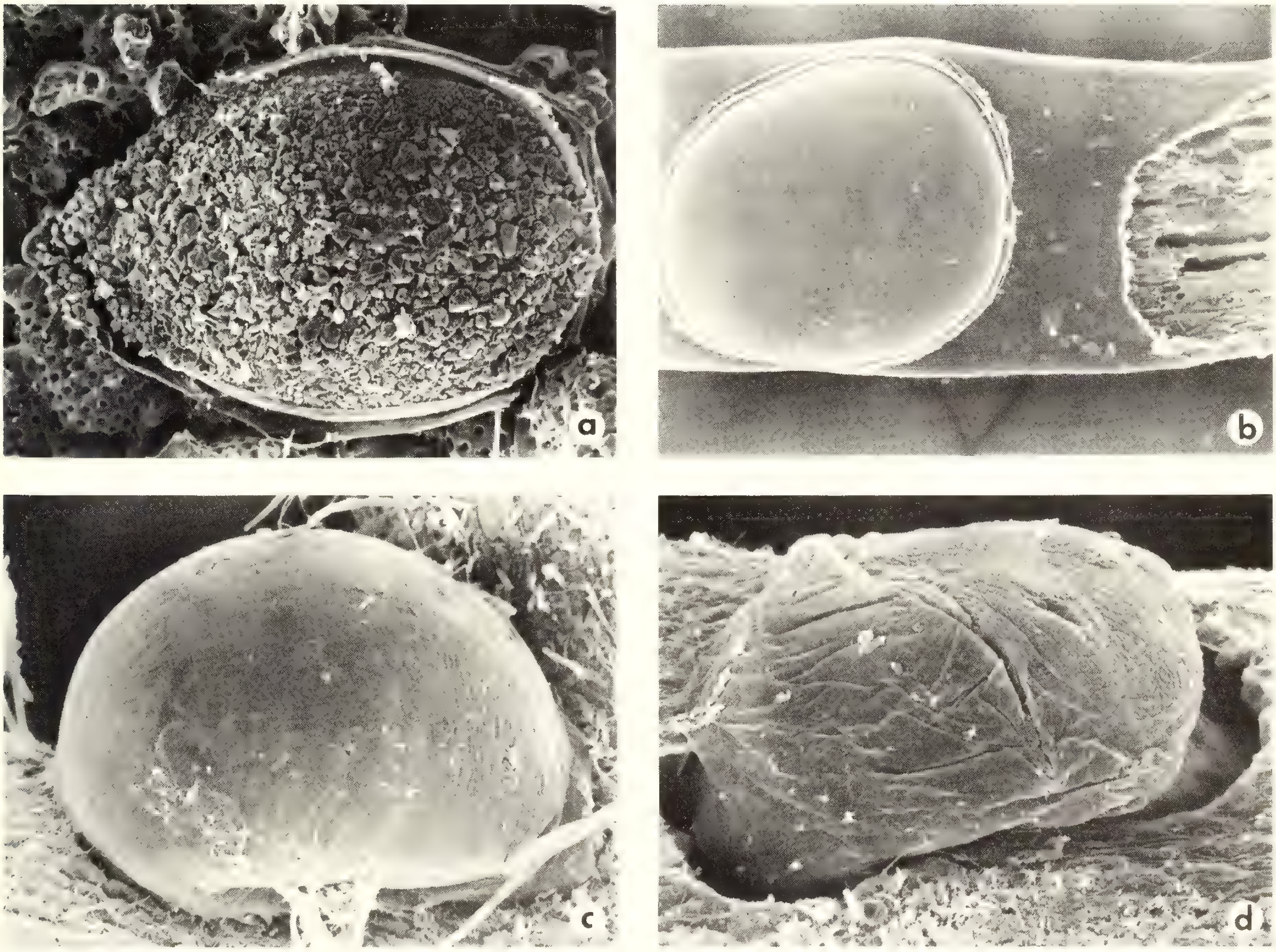

Fig. 1. SEM of prosobranch egg capsules attached to selected substrata. (a) *Puperita pupa* capsule on *Millepora*, apical view. Horizontal field width = 0.79 mm. (b) *Smaragdia viridis viridemaris* capsule on *Halodule*, apical view. Horizontal field width = 2.29 mm. (c) *Alvania auberiana* capsule on a rhodophyte, side view. Horizontal field width = 0.54 mm. (d) *Rissoina catesbyana* capsule partially buried in a rhodophyte, side view. Horizontal field width = 0.60 mm.

24-hours acclimation, and like those in splash pools, selected holes in calcium carbonate substrata. Between one and five egg capsules that closely resemble in shape those of *Neritina reclivata* (Say, 1822) (described by Andrews, 1935) were deposited daily. In outline, capsules of *Puperita pupa* were ovate, usually with one end narrower (Fig. 1a), or they conformed to the contour of the hole. Each was constructed of two obvious laminae fused near the edges, forming a lenticular structure enclosing embryos in albumen. Whether a continuous inner lining existed, like that of *Smaragdia viridis viridemaris* Maury, 1971 (described in the next section), was not determined. The basement lamina was disproportionally larger in area because it extended deep into the hole occupied by the capsule. Structurally, it included minute spherules or granules and a pore or suture at one end somewhat similar to sutures of *Neritina virginea* (Linné, 1758) or *N. reclivata* as reported by Andrews (1935). Peripherally, there was a thickened, brown-pigmented zone marking the point of fusion between apical and basement laminae. The brown pigment may be homologous to the adhesive material of *Smaragdia viridis viridemaris*. The apical laminae were convex (as shown in Fig. 1a), flat, or concave, depending on substratal configuration. As with *S. v. viridemaris*, the apical lamina fused peripherally with the basement lamina, forming an obvious coping or collar (defined by Andrews, 1935) not attached to the substratum (Fig. 1a). *Puperita pupa*, like most neritids, covered its egg capsules with particles from a crystal sac. The white, irregular particles appeared to be fragments of the calcium carbonate substratum ingested during feeding. They were often applied haphazardly or unevenly and overlapped the double-layered collar (Fig. 1a). Capsules with almost no additions from the crystal sac were found in splash pools. Capsular dimensions are given in Table 3. Capsules from the field contained 11 to 19 embryos ($\bar{X} = 15$) in albumen. The presence of free yolk or degenerate oocytes was not established. Pattern of development and larval morphology suggest that *P. pupa* has a planktotrophic veliger. After hatching, these could disperse from splash pools only when flooded by storm-driven waves.

Smaragdia viridis viridemaris Maury, 1917
(USNM 836976)

Emerald nerites observed in the laboratory from February to April, 1985, fed voraciously on new leaf tissue of *Halodule wrightii* and *Thalassia testudinum* and deposited daily (for 28 days) one to six egg capsules ($\bar{X} = 3$) adjacent to feeding sites (Fig. 1b). No capsules were attached to portions of leaves that were encrusted with epiphytes or damaged by feeding. Capsules were also attached to glass or polystyrene culture dishes, and infrequently, to the surface film to which they adhered until disturbed. Then the floating capsules sank immediately.

Egg capsules of *S. v. viridemaris* had the same general appearance of *Puperita pupa* capsules (described earlier) or *Neritina* sp. capsules (see Andrews, 1935) when last mentioned nerites did not apply the contents of the crystal sac. The transparent, pale yellow capsules, enclosing yellow embryos, were slightly pustulate in shape and ovate or occasionally round in outline, and totally lacked spherules or debris on the surface (Fig. 1b). Bandel (1982) briefly described similar egg capsules with green ova for this species from Colombia. Sections were lenticular with a convex apical lamina and a flat basement lamina closely applied to the substratum (Fig. 4a). The capsule wall was layered, with a thin, inner lamina enclosing embryos suspended in granular albumen. The outer layers varied in thickness with the convex, apical lamina being at least twice as thick as the basement lamina. Marginally, the apical and basement laminae met only on the periphery to form a thin coping or collar (defined by Andrews, 1935) not attached to the substratum. The basement lamina was also marked by a suture or pore (Fig. 2a), as are most neritid capsules. Under the basement lamina, there was another extremely thin, differentially stained layer of adhesive material, applied directly to the substratum. This material was thicker at the periphery where it extended a short distance under the coping surrounding the capsule (Fig. 4a). Fretter (1946) described adhesive layers covering both sides of *Theodoxus fluviatilis* (Linné, 1758) capsules; the outer layer served to attach material from the crystal sac, while the inner layer cemented the capsule to the substratum. As with *Puperita pupa*, the coping and the extended edge of adhesive material formed a double layered margin or collar around each capsule (Fig. 2a, b). Capsular dimensions are given in Table 3. Capsules deposited in the laboratory contained 70 to 90 embryos ($\bar{X} = 81$). Just prior to hatching, the planktotrophic veligers (described from the plankton by Robertson, 1971) had two to four obvious, red-pigmented cells on either side of the foot and pale yellow digestive glands (colorless stomach). At hatching, parts of the coping surrounding the capsule fell away and the apical layers separated from the basement layers, except at one end. Bandel (1982) showed how at hatching the halves of the inner capsule separate from the apical and basement laminae and help to push larvae out of the capsule.

Littorina mespillum (Mühlfeld, 1824)
(USNM 836983)

Mature adults were collected between February 26 and March 6, 1985, from the same yellow zone splash pools on limestone platforms near South Bimini, Bahamas, that produced the *Puperita pupa* specimens described earlier. Spawning occurred after four days in the laboratory. The number of planktonic capsules released by individual females was not determined, but the overall response suggested that during an extended breeding season this species could release thousands, as Borkowski (1971) reported for several Floridian littorinids.

The planktonic egg capsules of *L. mespillum* had gross structural resemblance to unattached capsules of other littorinids (the extensive literature was cited by Bandel and Kadolsky, 1982). In size, averaging 0.26 mm across the widest part of the basal disk, *L. mespillum* capsules approximated planktonic capsules of six Floridian littorinids described by Borkowski (1971). The greatest volume of the transparent

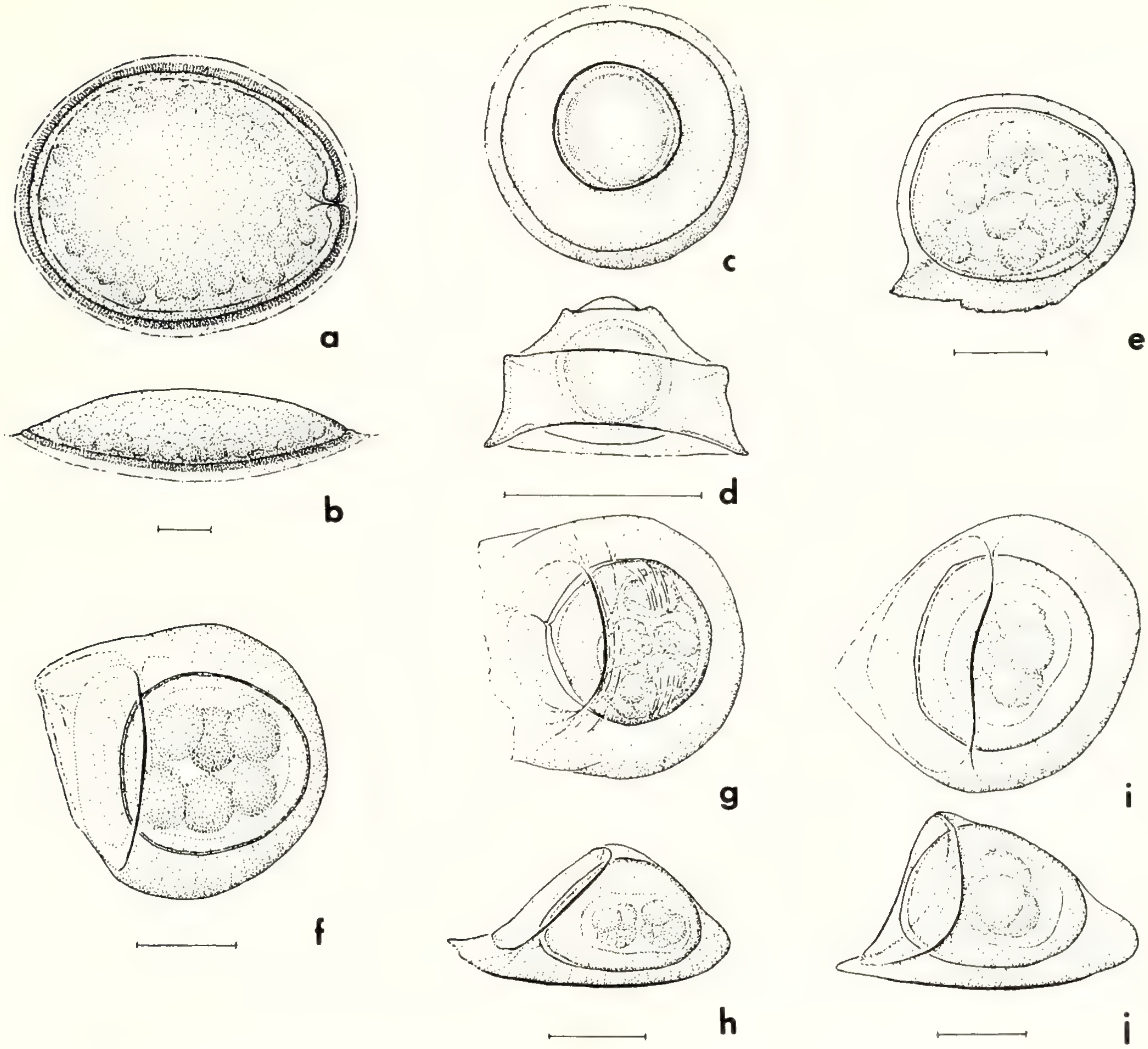

Fig. 2. Views of prosobranch egg capsules prepared with reflected and transmitted light. Magnification bars = 0.2 mm. (a) *Smaragdia viridis viridemaris*, apical view. (b) *S. v. viridemaris*, side view. (c) *Littorina mespillum*, apical view. (d) *L. mespillum*, side view. (e) *Alvania auberiana*, side view after expansion of innermost lamina. (f) *Rissoina catesbyana*, apical view. (g) *R. bryerea*, apical view. (h) *R. bryerea*, side view. (i) *Zebina browniana*, apical view. (j) *Z. browniana*, side view.

capsule was in the basal disk, where a flaring edge marked its widest point (Figs. 2c, d). From this point, the sides of the disk tapered very gradually across its width and then tapered abruptly to form a dome. Most capsules had a ridge or ring around the apex of the dome (Fig. 2d). A single embryo (average diameter = 0.11 mm), enclosed in an ovarian membrane and surrounded by albumen, was centrally positioned within the viscous capsular fluid. Of the species described by Borkowski (1971), Pilkington (1971), and Bandel (1974), *L. mespillum* capsules resemble most closely those of *L. meleagris* and *Melarpha cincta* (Quoy and Gaimard, 1833). Both species have domes with one more encircling ridge or ring than *L. mespillum*, as well as having flatter apexes.

Bandel (1974) suggested that Lewis' (1960) description of *Puperita pupa* capsules actually referred to *L. mespillum.* Lewis' figure of specimens from Barbados had a narrower and curved basal disk and a less prominent dome than seen in the material from Bimini. Lewis reported that planktotrophic veligers hatched after two days. As with *Puperita pupa*, egg capsules or swimming veligers of *Littorina mespillum* can be released from splash pools only when flooded by storm-driven waves.

Alvania auberiana (Orbigny, 1842)
(USNM 836984)

This West Indian rissoid, which is abundant in seagrass beds, paired and spawned from February through May, 1985. When given a choice of substrata for oviposition (*Laurencia poitei*) and other rhodophytes, *Halodule wrightii*, calcium carbonate, and the culture dish), 93% (N = 13) selected sites either in a bifurcation of an algal thallus or on a *Halodule* leaf adjacent to or among large branching epiphytes. No capsules were attached to calcium carbonate substrata (bivalves or conspecific shells) or to the culture dish. *Alvania punctura* (Montagu, 1803) will deposit egg capsules on conspecific shells (Lebour, 1934). Figure 1c is an electron micrograph showing a typical, newly deposited capsule. In the laboratory with sufficient food (Table 2), one or two capsules were deposited daily for at least four days. Spawning ceased when abundant food was not available. Several communal spawning sites were observed with as many as six capsules included. It is possible that this activity was caused in the laboratory by competition for available spawning sites.

The colorless, transparent egg capsules appeared to be hemispherical or almost spherical when viewed apically or ovoid when viewed laterally. Each was attached by a basal membrane that extended to one side and often was folded and conformed to substratal topography (Figs. 1c and 2e). Externally, capsules were covered with adhesive material that accumulated detritus as development progressed (Fig. 4b). Similar hemispherical egg capsules were described by Lebour (1934) for *A. punctura*, with some variation toward lenticular shape noted, and by Fretter and Graham (1978) for *A. abysicola* (Forbes, 1850), based on a drawing by G. Thorson. This illustration also included obvious detritus on the capsule and a thin, apical area that may facilitate hatching. The latter was not observed in *A. auberiana*, but there was a wrinkled area on one side (Fig. 1c) where the larvae eventually exited.

In section, *A. auberiana* capsules had an outer envelope or wall composed of two closely applied laminae (Fig. 4b). The outermost layer was actually a matrix that thickened basally where it served to attach the capsule to the substratum. The inner layer was thinner, optically denser, and similar to the optically dense laminae of rissoinid capsules (see later sections). Newly deposited capsules had 8 to 14 pale white ova ($\bar{X} = 12$) tightly enclosed within a thin, granular lamina with little obvious albumen. As development progressed to the veliger stage, the granular lamina expanded until it was forced against the outer envelope (Fig. 2e). Rasmussen (1973) found a similar innermost lamina in *Rissoa albella* Loven, 1846, that was connected to the outer envelope in two locations. If connections exist in *A. auberiana*, they were hidden in the basal area. Rasmussen (1973) also observed that the innermost lamina in *R. albella* ruptured prior to hatching and the embryonic veligers filled the whole capsular lumen. Capsular dimensions are given in Table 3. Planktotrophic veligers hatched from capsules in seven days through a ragged-edged hole that appeared on one side.

Rissoina catesbyana Orbigny, 1842
(USNM 836982)

Specimens of *Rissoina catesbyana* were collected from St. Joseph Bay (northwest Florida) in January and May, 1985. Pairing by January specimens was infrequent; no egg capsules were observed in the laboratory for two weeks following collection. May specimens from the same location paired frequently and spawned within 24 hours. In the laboratory, spawning *R. catesbyana* excavated holes in algal thalli, especially rhodophytes including *Laurencia obtusa*, and daily deposited one or two capsules (Fig. 1d). Excavations were often deep enough to cover a capsule, thus they are easily overlooked. On fragments of *Laurencia* used as spawning sites in the laboratory, 88% (N = 17) of the capsules were hidden in holes. Spawning sites were not concentrated on particular portions of a thallus; however, females did exploit broken or damaged areas to initiate excavations. No capsules were placed on *Halodule* leaves, shells, or on culture dishes.

Of the rissoinids included in this report, *R. catesbyana* showed the greatest variation in capsular shape, apparently due to distortions caused by cryptic habits. Transparent, colorless, and slightly wrinkled capsules with white ova positioned directly on the surface of an algal thallus were used as the basis for this description. Gross structure, which was quite similar to *R. bryerea* (described in the following section), was lingulate or wedge-shaped, with a distinct apical ridge extending at right angles to the long axis (Figs. 1d and 2f). On the side distal to the spawner (the side placed on the bottom of an excavation), the capsules were rounded, while the proximal side was more vertical, flattened, and tapered basally to a point that usually projected to one side (Fig. 2f). The more vertical and flattened side, which had a different surface texture than the rest of the capsule, served as an escape aperture. In apical view, several capsular laminae were apparent; one in particular was quite distinct (Fig. 2f). Sections revealed an outer envelope like that of *Alvania auberiana* previously described. The outer lamina of the envelope was actually a thick matrix bordered internally by a distinct, optically dense lamina (Fig. 4c). Within, the embryos were suspended in clear albumen surrounded by an innermost granular lamina bordered by a vesicular zone. The vesicules disappeared as the embryos grew and expanded the granular lamina toward the optically dense lamina. Only two capsular dimensions are given in Table 3 because most *R. catesbyana* capsules could not be dislodged from their crypts for measurement without altering their shape. *Rissoina catesbyana* egg capsules contained four to eight embryos ($\bar{X} = 6$) that hatched as planktotrophic veligers after at least eight days of intracapsular development. Moore (1969) also reported observing planktotrophic larvae.

Rissoina bryerea (Montagu, 1803)
(USNM 836980)

Specimens from southern Florida, collected during April and May, 1985, spawned immediately in the laboratory. With one exception, egg capsules were deposited on culture dishes (at the intersection of the side and bottom, between the lid and the side, or inverted on the cover). No holes were excavated in available algal thalli, nor did the females use bivalve shells or *Halodule* leaves. One capsule was found on a *Laurencia* thallus in a crevice formed by a fracture.

Egg capsules of *Rissoina bryerea*, like those of *R. catesbyana*, were transparent, colorless, contained white embryos, and had the rissoinid lingulate or wedge shape with a distinct apical ridge extending at right angles to the long axis (Figs. 2g, h and 3a). The rounded side (distal to the spawner) in some specimens had folds in the surface layer. The proximal side, which served as an escape aperture, sloped from the apical ridge to a broad basal area. In a few specimens, the basal area tapered to a point like most capsules of *R. catesbyana* or *Zebina browniana* (Orbigny, 1842). Surface texture of the layer through which veligers escape was different from the remaining capsule. When viewed apically, a distinct inner lamina and a zone with less dense albumen surrounding the embryos were visible. Sectioned capsules showed a layered outer envelope in which the outer lamina was actually a matrix surrounding an optically dense inner lamina (Fig. 4d). Within the optically dense lamina, the embryos in thin, clear albumen were surrounded by a substantial, granular lamina that separated them from the surrounding vesicular zone. In this species, the vesicles were larger than those of *R. catesbyana* previously described. As the embryos developed, the granular lamina expanded toward the optically dense lamina. Capsular dimensions are presented in Table 3. Egg capsules contained four or five large embryos that hatched as planktotrophic veligers in 11 days.

Zebina browniana (Orbigny, 1842)
(USNM 836981)

Specimens collected from southern Florida during April and May, 1985, paired and began to spawn immediately after collection. One or two egg capsules were consistently deposited in two locations: on the culture dishes (inverted under the cover or between the cover and the side) and on the under side of *Halodule* leaves heavily encrusted with epiphytes. This species appeared to prefer to deposit capsules under an object.

Zebina browniana has typical rissoinid egg capsules quite similar to *Rissoina catesbyana* and *R. bryerea*, only larger (see Table 3), enclosing a single, yellow-white, yolk-

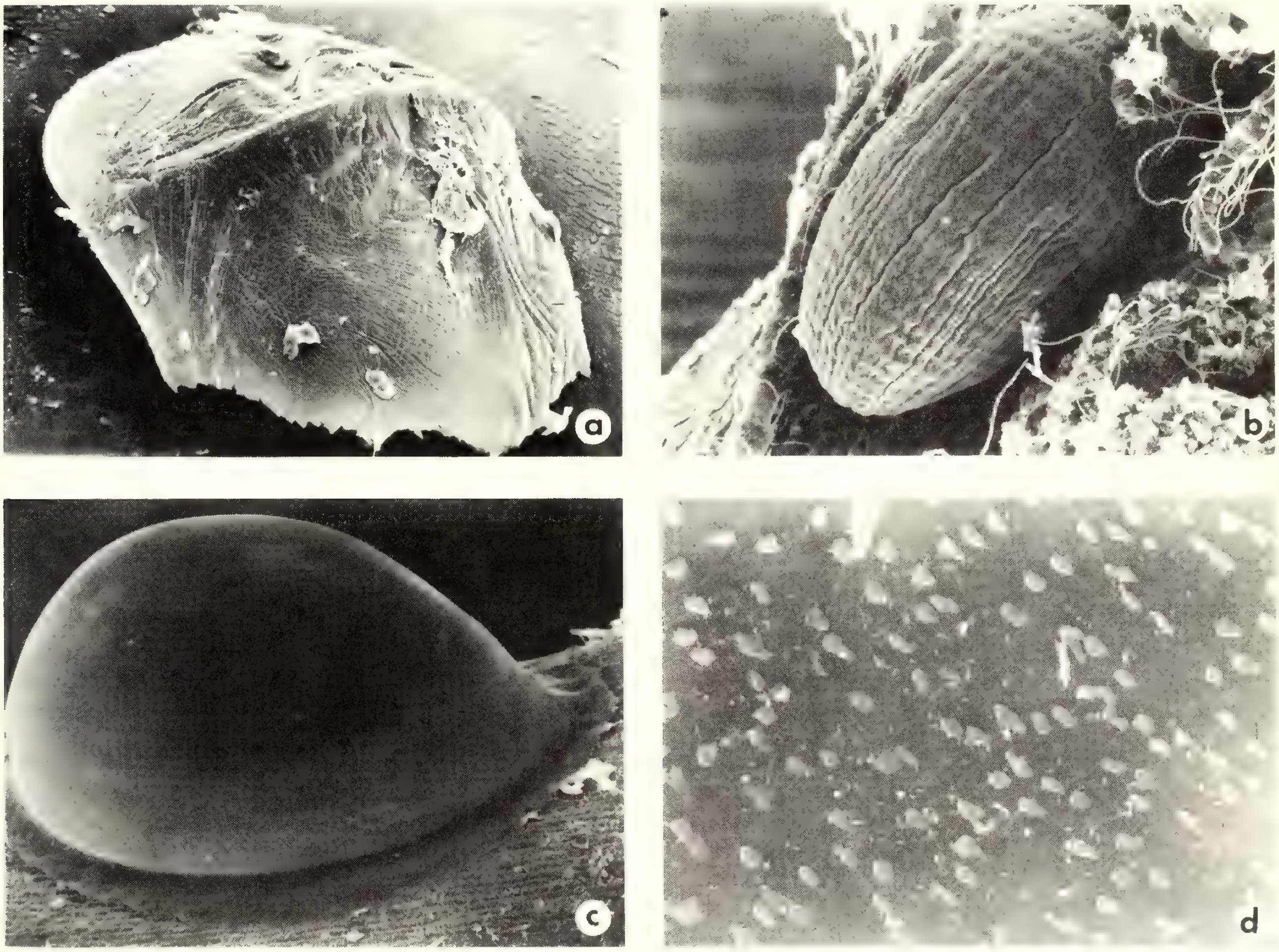

Fig. 3. SEM of prosobranch egg capsules attached to selected substrata. (a) *Rissoina bryerea* on polystyrene, view of side where the escape aperture opens; edge of specimen is fractured. Horizontal field width = 0.47 mm. (b) *Rissoella caribaea* on a rhodophyte. Horizontal field width = 0.65 mm. (c) *Granulina ovuliformis* on *Halodule*, side view. Horizontal field width = 0.97 mm (d) *Marginella aureocincta*, granules on the apical lamina. Horizontal field width = 0.017 mm.

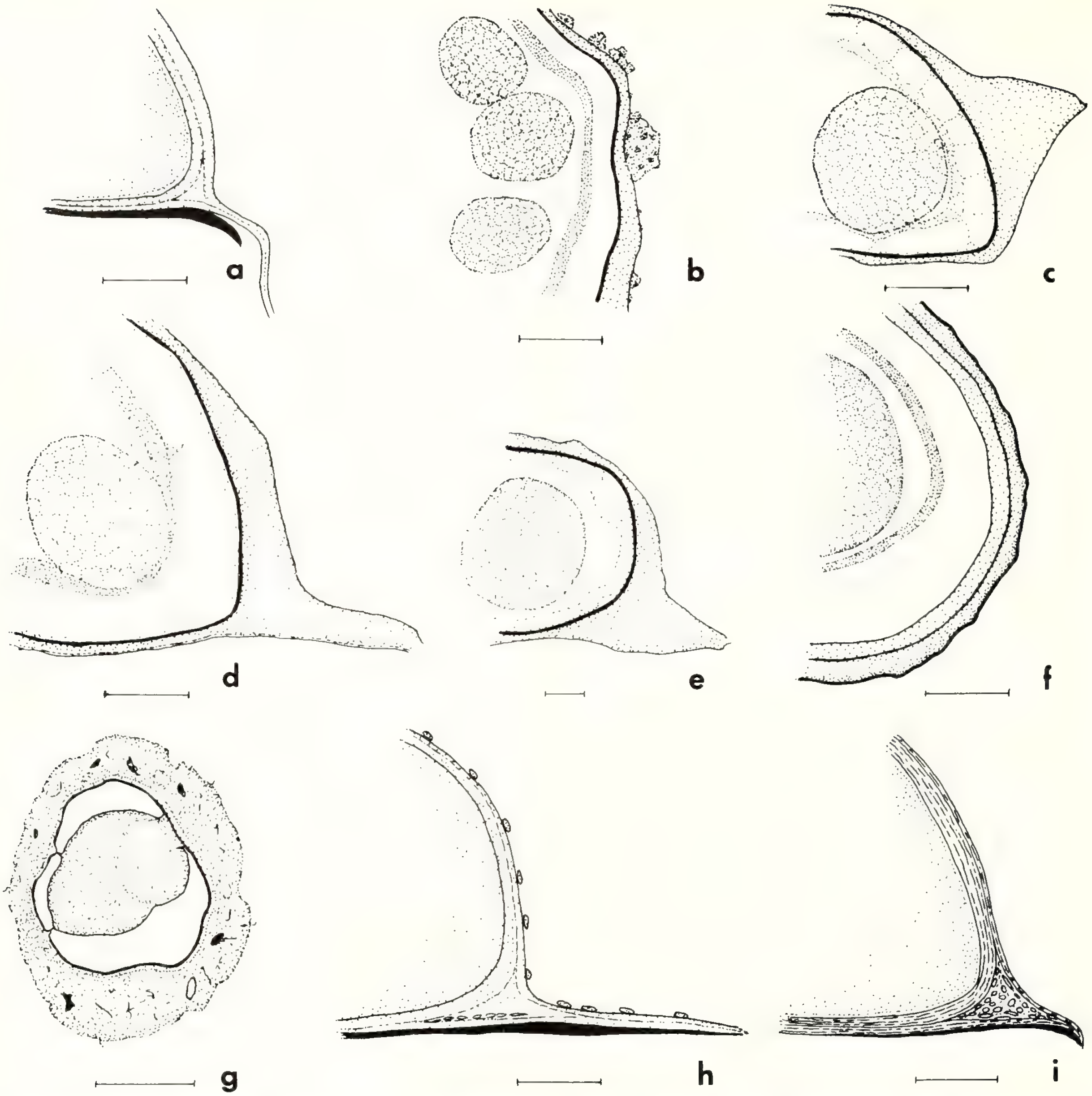

Fig. 4. Partial sections (except g) of prosobranch egg capsules showing various laminae. Basal laminae are positioned toward the bottom of the page. Optically dense layers are the broadest, solid lines. Some capsules contain embryos. Magnification bars = 0.05 mm. (a) *Smaragdia viridis viridemaris* (b) *Alvania auberiana*, outer lamina with detritus. (c) *Rissoina catesbyana*. (d) *R. bryerea*. (e) *Zebina browniana*. (f) *Rissoella caribaea*. (g) *Caecum nitidum*, section of a whole capsule surrounded by feces. Note that the embryo is attached to the capsule. (h) *Marginella aureocincta*, outer lamina with irregular granules oriented toward the capsular apex. (i) *Granulina ovuliformis*, spongy region located at the confluence of the major laminae.

filled ovum that hatched as a crawling juvenile in 28 days. Gross structure of the tansparent and colorless capsules was lingulate or wedge-shaped with a pronounced apical ridge arranged at right angles to the long axis (Figs. 2i, j). The apertural area was broad, while the basal area usually tapered to a central point below it, somewhat like capsules of *Rissoina catesbyana*. In section, the outer envelope was composed of a matrix surrounding an optically dense lamina (Fig. 4e). As in the other rissoinids studied, an innermost granular lamina surrounded the embryo, which was suspended in thin albumen. Few obvious vesicles were apparent between the innermost lamina and the optically dense lamina (Fig. 4e).

Rissoella caribaea Rehder, 1943
(USNM 836986)

Adult specimens from southern Florida and Bimini, Bahamas, were collected and observed between February and May, 1985. Egg capsules were first deposited by

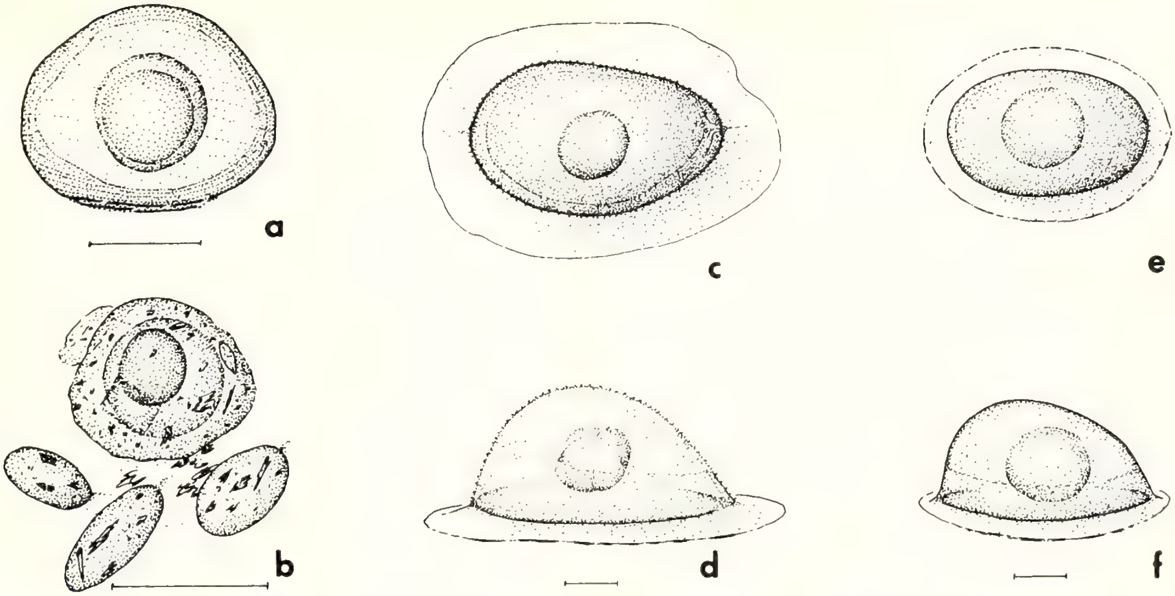

Fig. 5. Views of prosobranch egg capsules prepared with reflected and transmitted light. Magnification bars = 0.2 mm. (a) *Rissoella caribaea*, side view. (b) *Caecum nitidum* capsule surrounded by a fecal layer with diatom frustules and three fecal pellets. (c) *Marginella aureocincta*, apical view. (d) *M. aureocincta*, side view. (e) *Granulina ovuliformis*, apical view. (f) *G. ovuliformis*, side view.

specimens from Bimini in early March. Floridian specimens spawned in late March and April. Bahamian specimens deposited egg capsules in dense mats of *Amphiroa* sp. or in mats of epiphytes on *Laurencia* sp.. Floridian specimens used epiphytic mats on *Laurencia* sp.. Specimens from both locations cleared epiphytes from the site selected for oviposition. No spawn was attached to seagrass leaves, calcium carbonate substrata, or culture dishes.

Egg capsules of *Rissoella caribaea* were elongate and laterally flattened ovoids with furrowed bases (Figs. 3b and 5a). These general features are known for *R. diaphana* and *R. opalina* (Fretter, 1948). When viewed by light microscopy, capsules appeared faintly cancellate, a character that was more obvious when electron microscopy was used (Fig. 3b). On the longitudinal axis, some cancellations were accented by deep furrows. In section, the primary capsule wall was composed of at least two laminae. The outer one had an optically dense outer surface that could constitute a third lamina (Fig. 4f). The dense surface formed the cancellated sculpture of the primary capsule wall. Primary capsules from Florida contained one or two embryos; those from the Bahamas had three or four embryos. Each yolky, yellowish embryo was surrounded by a thin secondary capsule, possibly the vitelline membrane, that also enclosed some fluid. Fretter (1948) identified this fluid as albumen. Spherical secondary capsules were suspended in the thin fluid of the primary capsule. As development progressed, the inner spheres swelled to fill the lumen of the primary capsule. Embryos passed through a veliger stage, and after 18 days, hatched through a slit formed in a longitudinal furrow on the primary capsule as grayish-white, crawling juveniles. Capsular dimensions for a combined sample of Bahamian and Floridian specimens are presented in Table 3.

Caecum nitidum Stimpson, 1851
(USNM 836985)

Caecum nitidum released unattached, demersal egg capsules in the laboratory from January through May, 1985. After 24-hours acclimation during which few capsules were released, spawning progressed unabated in populations of adults provided with sufficient food (Table 2). Daily estimates of production were as high as six capsules per female. Released capsules sank rather quickly and became entangled and adhered to algae and detritus. In habitats with strong currents these capsules could be transported short distances.

Egg capsules of *C. nitidum*, like those described for other caecids by Götze (1938), Marcus and Marcus (1963), and Bandel (1976a), were thin-walled spheres, probably ovarian in origin, enveloped in a nearly opaque coating, 0.02 to 0.04 mm thick, attached to the capsule by a thin matrix (Fig. 4g). The previously mentioned authorities believe the opaque material to be of fecal origin. Embedded in the coating were diatoms, spicules, and fragments of organic material that appeared identical to that found in fecal pellets (which, as shown in Figure 5b, were often longer than egg capsules.) Females frequently deposited capsules with little or no fecal layer. In section, early in development, embryos appeared to be attached to the capsular walls (Fig. 5b). The expanding inner lamina reported by Bandel (1976a) was not observed, but could have been present. Average capsular diameters (with and without the fecal layer) are given in Table 3. Planktotrophic veligers escaped from the capsules after two to three days.

Marginella aureocincta Stearns, 1872
(USNM 836974)

During April and May, 1985, *Marginella aureocincta*, when provided with abundant food (Table 2), deposited one capsule per spawning event on polystyrene culture dishes. Seagrass leaves, algal thalli, and calcium carbonate substrata were not utilized for spawning.

Egg capsules were inflated, elongated, plano-convex structures with wide bordering layers (Figs. 5c, d) typical of marginellids (see Knudsen, 1950; D'Asaro, 1970; Bandel, 1976b). The whole capsular surface and bordering area were covered by raised, irregular granules mostly arranged with their long axes projecting toward the capsular apex (Figs. 3d and 4h). A faint discontinuity zone around the lower third of the capsule was visible when viewed by light microscopy, but not by electron microscopy. A similar zone, described by Knudsen (1950) in *Marginella marginata* and Bandel (1976b) in *Hyalina avena* (Kiener, 1834) and very obvious in *Granulina ovuliformis* (see the following section), probably occurs in most marginellids with plano-convex capsules, although it may be indistinct prior to hatching. Sectioned capsules had thin, dense walls composed of three distinct laminae, each formed from multiple, indistinct layers (Fig. 4h). The innermost lamina surrounded granular albumen and a single embryo. The outer apical lamina extended over the convex surface and the bordering area where it was fused to a basal lamina that lined the bottom of the capsule. A dense, adhesive layer, thickened near its outer edge, attached the capsule to the substratum (Fig. 4h). Capsular dimensions are given in Table 3. Development was direct to a crawling, juvenile stage. Hatching occurred after 35 days when the capsule separated from its base along most of the discontinuity zone.

Granulina ovuliformis (Orbigny, 1841)
(USNM 836973)

Adults observed intermittently from January began to spawn in late March, 1985. *Granulina ovuliformis*, an active predator, spawned only when food (Table 2) was continuously available. Only eight spawning events were recorded, during which single capsules were deposited on clean *Halodule* leaves.

Egg capsules were typical of most marginellids (see Knudsen, 1950). Each, with a single, large white embryo, was an inflated, elongated and rather transparent, plano-convex structure with a narrow bordering area (Figs. 5e, f). The apical area was completely smooth, even when viewed by electron microscopy (Fig. 3c). Surrounding the lower third, there was a discontinuity zone with indistinct patchy features (Fig. 3c). In *Marginella aureocincta*, the apical edge of this zone served as a fracture plane through which juveniles hatched. In section, capsules had walls constructed of three, very distinctly multilayered laminae (Fig. 4i). The inner lamina completely enveloped dense albumen and the embryo, just as in *M. aureocincta*. The outer lamina covered the apical surface and extended onto the flat border where it fused to the basal lamina. A very thin adhesive layer attached the capsule to the substratum. Around the lower edge of the convex portion at the confluence of the three structural laminae, there was a spongy zone (minute, fluid-filled pockets; Fig. 4i). Capsular dimensions are presented in Table 3. Hatching was not observed after 15 days. By comparing the pattern and rate of development with *M. aureocincta*, one can estimate that a crawling juvenile should hatch in approximately 30 days.

DISCUSSION

Two aspects of prosobranch encapsulation were addressed in this report: selection of specific substrata or locations for oviposition, and external and internal capsular structure. Even within the restraints imposed by the culture techniques, it was immediately obvious that each species with attached egg capsules did select, repetitively, specific substrata or locations for oviposition.

For most marine prosobranchs, use of a particular substratum for oviposition is not entirely a fortuitous process, it can influence survival of encapsulated embryos; thus, specific strategies have evolved. Many neogastropods, *Cantharus multangulus* (Philippi, 1848), *Murex fulvescens* Sowerby, 1834, or *Urosalpinx perrugata* (Conrad, 1846) (see D'Asaro, 1986), require, initially at least, some anchorage free of debris and poorly attached sessile organisms, and elevated above soft, potentially suffocating substrata. When sites are limited, novel choices must be made, for example, use of conspecific shells, egg capsules of other gastropods, or arthropod exuviave. Species spawning directly on soft substrata have evolved strategies to prevent suffocation or to anchor egg capsules. Some position extremely flat capsules on sand (*Polystira barrettii*) (Guppy, 1866); Penchaszadeh, 1982). Others incorporate the substratum in the egg mass creating elevated, porous, and camouflaged structures that hold embryos on the surface (*Strombus* sp., Robertson, 1959; *Polinices* sp., Giglioli, 1955). A few bury several modified egg capsules in the sand to serve as an anchor and foundation for the remaining capsules (*Busycon* sp., personal observation; *Conus figulinus* Linné, 1758; Kohn, 1961).

Very small prosobranchs are faced with the same requirements to locate suitable substrata for oviposition as are larger species. But since most small prosbranchs, especially mesogastropods, have microscopic, less refractory and often individually deposited capsules, camouflage and cryptic habits are frequently evolved strategies. Camouflage can be passive, as illustrated by the flat, transparent capsules with yellow or green embryos that *Smaragdia viridis viridemaris* deposits on yellow-green seagrass leaves (Bandel, 1985), or the capsules of *Alvania auberiana* that remain adhesive after oviposition and accumulate detritus. Camouflage can also be active as with *Puperita pupa,* where the contents of the crystal sac reinforce the capsule and help it to conform in appearance to the surrounding substratum, or as with *Caecum nitidum*, where the egg capsules are covered with feces until they appear to be little more than fecal pellets.

Cryptic habits involving deposition of encapsulated ova are occasionally described for marine prosobranchs. *Lamellaria perspicua* (Linné, 1758) and related species hide capsules in holes rasped in compound ascidians (Fretter and Graham, 1962). Rissoinids have evolved somewhat wedge-shaped capsules that are hidden in holes. Their capsules are structured with a preformed escape-area that is directed toward an escape-route for veligers or juveniles. In culture, each rissoinid placed capsules in different locations (holes rasped in algae, corners of the culture dish, or inverted on the dish cover), choices that suggest each species selects slightly different spawning sites in their natural habitat. Other species studied were cryptic in that they hide egg capsules in dense algal mats (*Rissoella caribaea*) or in holes in limestone (*Puperita pupa*). Cryptic behavior by *P. pupa* probably protects their minute capsules from inadvertent damage caused by larger grazing neritids, littorinids, and cerithiids that occupy the same splash pools.

Small prosobranchs that make no effort to hide their spawn have evolved survival strategies based on using water currents for dispersal. Thousands of minute transparent planktonic capsules can be released by *Littorina mespillum* and most other littorinids (see Borkowski, 1971, and Bandel and Kadolsky, 1982).

The neogastropod strategy for small species may include cryptic habits during oviposition, e.g. *Calotrophon ostrearum* or *Conus jaspideus stearnsi* Conrad, 1869 (D'Asaro, 1986), but it also includes an increase in the refractory nature of laminae in the egg capsule. Both *Marginella aureocincta* and *Granulina ovuliformis* make no obvious attempt to hide their egg capsules, selecting only hard, unfouled substrata. Each species has exceptionally tough and resilient, multilayered envelopes with dense albumen that serve for 30 days or more as a buffer against the environment.

The second aspect of prosobranch encapsulation addressed in this report, capsular structure, can provide data useful in life-history and systematic studies. Neogastropod taxa with pedal capsule glands, e.g. *Eupleura caudata* (Say, 1822) (Tamarin and Carriker, 1967) often have species-specific characters. More frequently, especially for lower prosobranchs, it is possible only to identify familial or generic characters. The species in this report, in most cases, demonstrate that point.

Most lower archeogastropods are broadcast spawners with only ovarian encapsulation which is equivalent to a vitelline membrane (Fretter and Graham, 1962). In trochaceans, the ovarian encapsulations may be surrounded by gelatinous matrices arising from glands in the urogenital or pallial regions (*Calliostoma zizyphinum* Linné, 1758; Fretter and Graham, 1977). Tricoliids use the primitive, broadcast method for spawning as well as a range of simple encapsulating strategies such as secreting various mucopolysaccharides to connect ova together. No single spawning method appears to characterize tricoliids, but they do demonstrate evolution away from primitive broadcast spawning.

Unlike other archeogastropods, neritids have pallial encapsulation, as Fretter (1964) demonstrated with *Theodoxus fluviatilis*. She, as well as Andrews (1935), found the neritid egg capsule to be a lenticular structure made of apical and basal layers fused at the periphery and reinforced on the apical surface with particles from a crystal sac. Data on *Puperita pupa* and *Smaragdia viridis viridemaris* egg capsules help to confirm that these are familial neritid characters, but two points can be mentioned. The thin, inner sacculate lining of the *S. v. viridemaris* capsule, which Andrews (1935) illustrated for *Nerita peloronta* Linné, 1758 and *N. tessellata* Gmelin, 1791, and Bandel (1982) has shown for *Neritina virginea* and *N. clenchi* Russell, 1940, could be a character common to all neritids. Thus typical neritid capsules should be recognized to include ova in albumen enveloped by a thin lamina, and layered between a reinforced apical layer and a thin basal layer. As Bandel (1982) has shown, the thin-walled, inner sac splits at hatching and can help to push larvae from the egg capsule. The second point is that at least one neritid, *Smaragdia viridis*, does not use calcium carbonate spherules or fragments from its food to reinforce and camouflage its egg capsules. However, *S. viridis* does thicken the apical layer by adding capsular material.

In mesogastropod groups, where pallial encapsulating mechanisms are the rule, the littorinids show a range of encapsulation methods that Bandel (1974) categorized. Most, like *Littorina mespillum*, have planktonic egg capsules. Others attach ova in gelatinous egg masses to hard substrata or are ovoviviparous. Bandel and Kadolsky (1982) suggested that the littorinid egg capsule is of restricted taxonomic value within the family. It appears to be species-specific but can be used to characterize only some genera (*Nodilittorina*; Bandel and Kadolsky, 1982).

Rissoid capsules, typified by *Alvania auberiana*, include a wide variety of basic capsular shapes. Fretter and Graham (1978) used these descriptive terms for species in various genera: *Cingula*: hemispherical, lentiform; *Onoba*: egg-shaped, hemispherical; *Alvania*: hemispherical (with possible escape aperture); *Rissoa*: lens-shaped, hemispherical, lenticular with flattened basal margin, transverse suture, and oval plug at apex. Although the term "typical rissoid" is used in various reports referring to capsular shape, in fact, there does not appear to be a typical familial shape, and even the generic characters are variable. For example, the *Rissoa* capsule is very different from confamilial capsules as indicated by the transverse suture and oval plug at the apex, characters *Alvania auberiana* capsules do not have. At best, one can say that the generic characters for *Alvania* capsules are usually the hemispherical shape, to which should be added that the outer covering is actually a somewhat plastic, adhesive matrix surrounding a more dense lamina. The embryos are initially enclosed in an inner lamina that expands as they develop. This inner layer, collectively surrounding embryos, is shown in Lebour's (1934) figures of *A. punctura* capsules and also in her figures of other rissoid capsules. Thorson's figure (in Fretter and Graham, 1978) suggests *Alvania* sp. may have a preformed escape structure, which in *A. auberiana* could be little more than a wrinkled area on the side of the capsules.

Rissoinid capsules are more elaborate variations of the *Alvania* type. *Alvania* and most other rissoids attach capsules on the surface of the substratum; however, rissoinids have evolved wedge-shaped egg capsules that are placed in convenient crevices (*Rissoina bryerea, Zebina browniana*) or holes excavated in algae by the spawner (*Rissoina catesbyana*). The outer matrix is thicker than that of *Alvania* sp., but the laminar pattern is essentially identical, including an inner layer that expands as development progresses. Because the rissoinid capsules are usually placed in a constricted area, they have a zone where an escape aperture will form aligned with an opening in the substratum. Rissoinids have other structural characters, but because the matrix is so plastic, only the lingulate or wedge shape with an escape aperture at one end can be considered a familial character.

Rissoellids have capsules distinctly different from the *Alvania* sp. or rissoinid pattern. *Rissoella caribaea* has bilayered capsular walls hardened on the outer surface, thus it has obvious sculpture resembling that added to egg capsules by neogastropods with pedal capsule glands. An inner lamina collectively surrounding embryos is absent; instead each embryo is enclosed in a thin membrane, probably the vitelline membrane. These structural relationships appear to be characteristic of *Rissoella* spp.

Caecids, placed in Rissoacea by Moore (1962), lack most of the special laminae common to previously mentioned rissoaceans, but they do have an outer matrix composed mostly of feces. Each embryo, in an unattached capsule, is surrounded by what appears to be a vitelline membrane to which it is fused at several points initially. Pallial encapsulation probably involves adding only a thin outer matrix to serve as cement for an enveloping fecal layer. For caecids, the fecal-coated, unattached egg capsule is distinctive.

Marginellid egg capsules, as described by Knudsen (1950) have two general shapes: lenticular with short stalk on one edge for attachment, and plano-convex with the flat side used for attachment. All have direct development. *Marginella aureocincta* and *Granulina ovuliformis* have the plano-convex structure, which is the most common and distinctive type in the family.

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ARE THE CONTENTS OF EGG CAPSULES OF THE MARINE GASTROPOD *NUCELLA LAPILLUS* (L.) AXENIC?

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ABSTRACT

The fluid from egg capsules of *Nucella lapillus* was found to be axenic when capsules contained living embryos. One hundred percent of excapsulated, pre-shelled embryos survived and developed for 21 days in sterile seawater to which antibiotics were added, while control embryos in unsterile, 0.45 μm filtered seawater died after four days. Providing early embryos with protection from bacteria may be one role for egg capsules. Since embryos could survive and develop outside capsules, the capsular fluid may not be necessary for growth of embryos of this species.

Thorson (1950) suggested that the fluid of gastropod egg capsules may have bacteriostatic properties, but subsequent studies on the fluid from capsules of four species (*Searlesia dira* [Reeve], *Nucella* [= Thais] *lamellosa* [Gmelin], *N. lima* [Gmelin]; Rivest, 1981; *N. lapillus* [L.]; Pechenik *et al.*, 1984) provided no evidence that the fluid deterred bacterial growth. However, if an egg capsule were impermeable to bacteria, and if the contents of that capsule were axenic when the capsule was formed, then an egg capsule could provide a bacteria-free environment for developing gastropod embryos, even though capsular fluid is not bacteriostatic. Recent studies have shown that eggs and sperm of the oyster, *Crassostrea gigas* (Thunberg) (Langdon, 1983) and the purple sea urchin, *Strongylocentrotus purpuratus* (Stimpson) (Manaham *et al.*, 1983) are axenic before discharge from the gonads. If the reproductive tracts of gastropods that make egg capsules are bacteria-free, then these gastropods could produce capsules with axenic contents.

The multilayered, vase-shaped egg capsule of the dog whelk, *Nucella lapillus*, has an outer layer of mucopolysaccharide, and the capsule wall is composed of a conchiolin-like material made of protein associated with polysaccharide (Bayne, 1968). Pechenik (1983) found that the tough capsule wall of this species is permeable to Na*Cl* and water, less permeable to amino acids, glucose, and sucrose, and appears to be non-permeable to large organic molecules (proteins and neutral polysaccharides; Bayne, 1968) found in the capsular fluid. If the capsule wall is impermeable to large molecules, then it is unlikely to be permeable to bacteria. Even small marine bacteria (0.5 μm in diameter; Hobbie *et al.*, 1977) are 150 times wider than the average globular protein.

Egg capsules of *N. lapillus* contain about 1.1 μl of fluid per embryo, and an average of 33.7 ± 16.3 embryos per capsule (Pechenik *et al.*, 1984). Packaged with the eggs that will develop into embryos are nurse eggs, on which the embryos feed during the first week of their development (Costello and Henley, 1971). After they have consumed the nurse eggs, the embryos resemble unshelled, yolk-filled sacs.

Pechenik *et al.*, (1984) attempted to rear both pre-shelled and shelled excapsulated embryos. Shelled embryos were reared in 0.45 μm filtered seawater for 29 days with 28% mortality, but 94.7% of the pre-shelled embryos died in 18 days. Pechenik *et al.*, (1984) did not determine whether bacterial contamination affected mortality of the pre-shelled embryos.

In this study I examined fluid and embryos from egg capsules of *N. lapillus* to determine whether the contents are bacteria-free and have raised pre-shelled, excapsulated embryos in autoclaved seawater with antibiotics to determine the influence of a bacteria-free environment on survival of the early embryos. Individuals are considered to be embryos until they escape from the egg capsule (Giese and Pearse, 1974). Embryos of *N. lapillus* hatch as crawl-away juveniles.

MATERIALS AND METHODS

Intertidal egg capsules of the prosobranch gastropod *Nucella lapillus* were collected from Nahant, Massachusetts during May and July, 1985, and kept at 14-16ºC in seawater filtered to 1 μm. Water was changed every other day.

To determine whether the capsular fluid of *N. lapillus* is axenic, fluid was removed from capsules and incubated overnight at room temperature in 5 ml of nutrient broth (0.20 μm filtered seawater, 0.25% yeast extract, and 1% peptone; Pechenik *et al.*, 1984). Presence of bacteria in the nutrient

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broth was determined by inspection. If no bacteria are present, the broth remains clear; contaminated broth becomes turbid and a thick scum of bacteria forms on the surface of the fluid within 24 hours.

Before fluid was removed, capsules were dipped in 95% ethanol to reduce bacterial contamination on the outer capsule surface. Dipping in 95% ethanol eliminates growth of surface bacteria for 24-36 hours. The fluid of newly deposited capsules is viscous (Pechenik, 1983) and clogs narrow gauge needles; a 21 gauge needle was therefore used to remove contents of newly deposited capsules. The fluid becomes non-viscous about five days after capsule deposition (Pechenik, 1983) and a 25 or 30 gauge needle was then used to suck out fluid while leaving embryos intact. After fluid was removed, capsules were cut open and the number of embryos per capsule and their developmental stage were noted.

Although it is unlikely that capsular fluid would be contaminated while embryos were axenic (or *vice versa*), it is possible that the techniques used to remove the fluid could contaminate capsule contents or kill bacteria in it. Therefore, embryos were also tested for contamination as a control. After being dipped in 95% ethanol, capsules were cut open and embryos were emptied into 0.2 μm filtered, autoclaved seawater. Embryos were added to the broth and incubated overnight at room temperature. Aliquots of water into which capsule contents had been emptied were checked before and after embryos were added to be sure water was sterile.

Fluid from capsules containing dead embryos was also checked for bacterial contamination. Capsules containing dead embryos can be recognized because when embryos of the genus *Nucella* die, they generally turn a purplish-pink color visible through the capsule wall (Spight, 1975; Gallardo, 1979; Pechenik, 1982, 1983). The fluid from capsules containing embryos dead at the time of collection, and from capsules in which embryos were killed by keeping the capsules overnight in deionized water, was examined for bacterial contamination as described above. Embryos from capsules kept in deionized water turned pink during exposure. Dead embryos were also tested for contamination.

To ensure that overnight exposure to deionized water did not kill bacteria, controls in which bacteria from the surface of capsules were cultured and then exposed to deionized water were run. After overnight exposure to deionized water, bacteria were added to culture broth, and the broth was checked after 24 hours.

To determine whether pre-shelled, excapsulated embryos could be raised in bacteria-free seawater, I passed seawater through a 0.20 μm Schleicher and Schuell filter, autoclaved the filtrate, and added the antibiotics penicillin (40 mg/l) and streptomycin (50 mg/l). Embryos were removed from five capsules by clipping off the capsule tops and emptying the capsule contents into sterile seawater. Eight embryos plus a portion of the nurse egg mass with embryos attached were placed in each of three replicate dishes containing 15 ml of the treated seawater. As a control, eight embryos were added to a dish of 0.45 μm filtered seawater that was not autoclaved and to which no antibiotics were added. Embryos were kept at 14ºC for up to 21 days and checked daily for mortality and development. Water was changed daily, and Day 1 was the day of excapsulation.

The fluid from egg capsules of two other gastropod species, *Buccinum undatum* (L.) (3 capsules) and *Thais haemastoma canaliculata* (Gray) (4 capsules) was also examined for bacterial contamination using techniques described above. *Buccinum undatum* capsules were collected from the walls of seawater tables at Northeastern University's marine lab, Nahant, Massachusetts. At the time fluid was sampled, embryos were still yolky and undeveloped, and fluid was slightly viscous. *Thasis haemastoma canaliculata* capsules were collected by Dr. C. D'Asaro in Florida and shipped to Massachusetts in late May. Two of the four capsules examined were a clear, creamy color and contained shelled embryos. Two capsules were darker brown, indicating that capsules were older and embryos were ready to emerge (R. Dobberteen, pers. comm.).

Capsular fluid and embryos were manipulated using sterile glassware in a sterile hood.

RESULTS

Fluid from capsules of *N. lapillus* containing living embryos was axenic in all cases examined. Of the 17 capsules containing pre-shelled to fully shelled embryos, none had fluid containing bacteria that grew in the nutrient broth. However, of 13 capsules containing dead embryos, the fluid within five capsules contained bacteria that grew overnight in the broth. None of the capsules exposed to deionized water contained bacteria, although bacterial contamination was found in fluid from field-killed capsules in which embryos were dead but not pink. Bacteria exposed to deionized water grew normally after being returned to broth and formed a scum on the broth surface within 24 hours.

Living embryos from three capsules were axenic, and the water into which the capsules were emptied was sterile. Dead embryos from one capsule out of five examined were contaminated with bacteria that grew in the broth. There were no capsules in which fluid was contaminated but embryos were not and *vice versa*.

All 35 of the pre-shelled embryos reared in seawater with antibiotics survived 21 days. In contrast, the eight control embryos were all dead by Day 4. By Day 2, one control embryo had expelled all the yolk it contained, and the two control embryos that survived through Day 3 also expelled their yolk between inspection on Day 2 and inspection on Day 3. (See Pechenik *et al.*, 1984 for a description of yolk expulsion.) The other control embryos disintegrated or had yolk protruding from parts of the body other than the mouth.

During the first six days of the experiment with excapsulated embryos, the number of embryos attached to the nurse egg masses changed. For example, on Day 3 no embryos in dish 1 were attached to the nurse egg mass, but on Day 4 two were on the mass, on Day 5 there were no embryos on the mass, and on Day 6 two embryos were again on the mass. These observations indicate that embryos could move off the masses and return later.

Over the 21 days of the experiment with excapsulated embryos, the embryos in seawater with antibiotics developed shells and eyes. By the end of the experiment, the shells of larger embryos had siphons, and shell lengths ranged from 453 μm to 1192 μm. Along with the 35 normal, yolk-containing embryos, there were 10 runts (embryos with little or no yolk) in the three dishes. These runts also survived the entire 21 days, but they did not differentiate noticeably.

Fluid from the three *Buccinum undatum* egg capsules was axenic. No bacteria were found in fluid from three of the *Thais haemastoma canaliculata* capsules. However, bacteria were found in one capsule. This was an older capsule with embryos ready to emerge; it may have been damaged.

DISCUSSION

Prosobranch egg capsules may provide protection against some predators (Pechenik, 1979; Perron, 1981) and salinity stress (Pechenik, 1982, 1983). Although the capsular fluid is not bacteriostatic, this study indicates that the egg capsules of *Nucella lapillus* provide a bacteria-free environment for developing embryos. In all capsules in which living embryos were found, capsular fluid and embryos were axenic. Death of embryos does not necessarily indicate that capsules are contaminated, suggesting that capsules with dead embryos may retain their impermeability to bacteria.

Generally, dead or moribund embryos of this species turn pink as a response to environmental stress (Pechenik, 1982, 1983), as embryos exposed to deionized water in this study did. However, two of the contaminated capsules contained dead embryos that had retained their creamy yellow color. Excapsulated embryos exposed to 0.45 μm seawater also retained their yellow color, even after death. It is possible that embryos that die from exposure to bacteria do not turn pink, unlike those that are exposed to salinity or temperature stress. Spight (1977) reports that hermit crabs cannot puncture the capsules of the West Coast muricid *Nucella lamellosa*. However, even a failed predation attempt may damage a capsule, allowing bacteria to enter and kill the embryos inside. Further work needs to be done to test this possibility.

While the embryos of some gastropod species can be raised outside their capsule (e.g. *Ilyanassa obsoleta* [Say]; Costello and Henley, 1971), previous attempts to raise pre-shelled embryos of *N. lapillus* have been unsuccessful (Pechenik *et al.*, 1984). In this study, 100% of the pre-shelled embryos survived and developed eyes and shells when reared axenically. This indicates two things: 1) pre-shelled embryos of this species are susceptible to bacteria found in seawater, and 2) the capsular fluid is not necessary for normal development of *N. lapillus* embryos. This second finding supports work done by Pechenik *et al.*, (1984) showing that the fluid from capsules of *N. lapillus* is not necessary for normal growth of developing embryos.

After *N. lapillus* embryos develop shells, they can be reared outside the capsule in non-sterile 0.45 μm filtered seawater (Pechenik *et al.*, 1984). This indicates that embryos loose their susceptibility to bacteria at some time during their development. Further research is needed to determine when *N. lapillus* embryos become resistant to bacteria, and if resistance is associated with development of the shell.

Preliminary work indicates that fluid from egg capsules of the gastropods *Thais haemastoma canaliculata* and *Buccinum undatum* is also axenic. More work needs to be done on other species to determine whether gastropod egg capsule contents are generally axenic. This study indicates that, even when the fluid from egg capsules does not have bacteriostatic properties, egg capsules themselves may protect against bacteria by providing an axenic microenvironment for developing embryos.

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THE EMBRYONIC CAPSULES OF NUDIBRANCH MOLLUSCS: LITERATURE REVIEW AND NEW STUDIES ON ALBUMEN AND CAPSULE WALL ULTRASTRUCTURE

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ABSTRACT

Nudibranch egg capsules are small (100-300 μm) transparent structures that surround the eggs inside a gelatinous egg mass. The capsules are produced by the albumen and/or capsule glands of the parent, and usually contain one or more embryos, sperm, and fluid that can contain albumen. In this paper I term albumen any material with a condensed granular ultrastructure observed between the embryonic surface and the inner capsule wall. Although aeolid nudibranchs are said to lack albumen, intracapsular albumen was observed in three species: *Aeolidia papillosa, Coryphella salmonacea,* and *Hermissenda crassicornis*. Preliminary ultracytochemical staining did not detect carbohydrates oxidizable with periodic acid in the intracapsular fluid of 14 day old preveliger *A. papillosa*. Intracapsular fluid from 1, 2, 4, 6, and 7 week old (= ready to hatch) *C. salmonacea* capsules all contained abundant albumen, suggesting that the albumen does not serve a major nutritive role in this species. Treatment of intact *C. salmonacea* capsules with various enzymes did not significantly increase capsule permeability to fixatives and embedding media or increase capsule puncturability. Capsule wall ultrastructure was relatively consistent within each of the six species examined. The capsule walls had no consistent layers and ranged in thickness from 0.07 μm in *H. crassicornis* to 4.5 μm in *Archidoris montereyensis.* Based on data available for the six species examined, capsule wall thickness was not obviously correlated with suborder, developmental type, days to hatching or numbers of embryos per capsule.

Embryos of all nudibranch molluscs develop within tiny, fluid-filled capsules. These capsules average 100-300 μm in diameter and are embedded in gelatinous egg masses (Hurst, 1967; Thompson, 1976). We know little about the formation, structure or adaptive value of either the capsules or the egg masses. The present paper reviews the relevant literature concerning capsule formation, contents, breakdown (at hatching), and adaptive value, and suggests avenues for future research. In addition, this paper presents recent observations on the ultrastructure and fate of the intracapsular albumen, on the ultrastructure of the capsule wall, and on the effect of enzymes on capsule wall permeability.

TERMINOLOGY

The term "capsule," as applied to nudibranch egg masses, is the nonliving spherical to ovoid organic container immediately surrounding the eggs and, as they develop, the embryos (Fig. 1). Therefore, this one structure is sometimes called the egg capsule during early development and the embryonic capsule during later development. Less commonly, this same container has been referred to as the membrane (Ghiselin, 1965), egg sac (Bayne, 1968), egg membrane (Thompson, 1976) or egg-case (Kress, 1971; Thompson, 1976). In giving dimensions of the encapsulated eggs of several opisthobranchs, Rasmussen (1944) occasionally referred to the capsule (diameter) as the uncleaved egg (diameter); he then termed "yolk" what we now call the egg.

In some species, a thin transparent tube called the secondary membrane (Thompson, 1958) surrounds the capsules (= primary membranes). Both of these layers are enclosed by a gelatinous egg mass.

Each capsule contains fluid, which is sometimes referred to in its entirety as albumen. Although albumen, a proteinaceous substance, can occur in this fluid, the fluid itself is more accurately referred to as the intracapsular (= capsular) fluid.

ORIGIN

The capsules are secreted by the female accessory glands of the hermaphroditic reproductive system. This cluster of female glands usually includes a proximal albumen gland and a distal mucous gland, separated by a membrane

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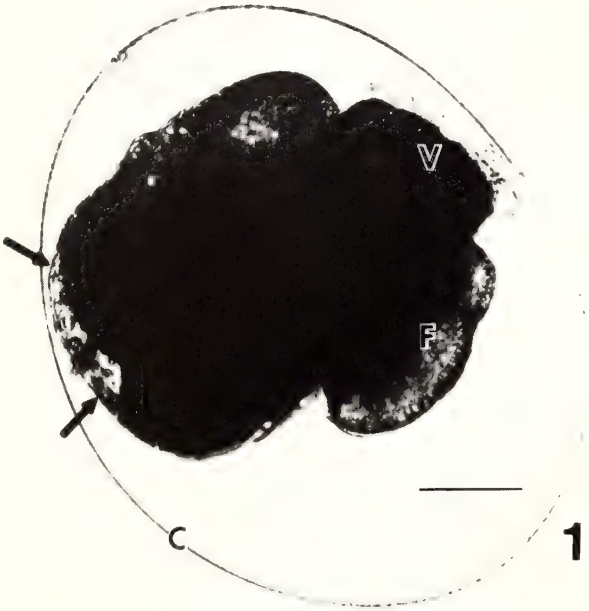


Fig. 1. Light micrograph of nudibranch embryo inside its turgid, fluid-filled capsule (C). The velum (V), foot (F) and part of the shell (arrows) of this six-week old *Coryphella salmonacea* embryo are visible through the transparent capsule wall. Bar = 100 μm.

gland or winding gland (Ghiselin, 1965; Kuzirian, 1973; Thompson, 1976; see complete review for all opisthobranch orders, by Hadfield and Switzer-Dunlap, 1984). During oviposition, a mixture of eggs and allosperm (sperm received during copulation) pass through and are coated by secretions of these glands. The most distal organ, the mucous gland, secretes a gelatinous egg mass that will surround the encapsulated embryos and attach them to the substratum.

The roles of the other more proximal organs are less certain and have rarely been studied. Chambers (1934) examined the reproductive system of *Embletonia fuscata* but could not distinguish the albumen-secreting region of the oviduct from the region that secretes the capsule wall. He referred to the capsule as a "thin but tough 'shell' coat" that is secreted by the "shell gland". However, the capsule of nudibranchs is not a shell and the term shell gland more commonly refers to the invaginated region of the embryonic shell field (see Eyster and Morse, 1984, for review). Lloyd (1952) fixed *Archidoris britannica* during oviposition to examine deposition of the "egg coverings" and concluded that only the intracapsular albumen was deposited by the albumen gland and that the gelatinous layers were produced by the mucus gland; she did not comment specifically on the origin of the capsules. Kuzirian (1973) examined *Coryphella salmonacea* individuals fixed in the act of oviposition and observed a fuzzy layer of 'albumen' (not a capsule) coating the oocytes as they passed through the albumen gland. In contrast, other authors have reported that the albumen gland secretes the capsule wall (Schmekel, 1971; Thompson, 1976); in particular, Schmekel (1971) emphasized that the albumen gland in nudibranchs secretes the capsule wall and "not a layer of protein between egg and capsule." The confusion about which organ secretes which product may occur because the region of the oviduct referred to as the albumen gland by one author may be histologically separable in another species or by a second author into two regions: a proximal area that secretes albumen, and a distal region that secretes the capsule wall. Also, part of this confusion probably arises from retention of the term "albumen gland" in species believed to lack intracapsular albumen (Ghiselin, 1965; Beeman, 1977). More studies of egg capsule deposition are needed to resolve this issue.

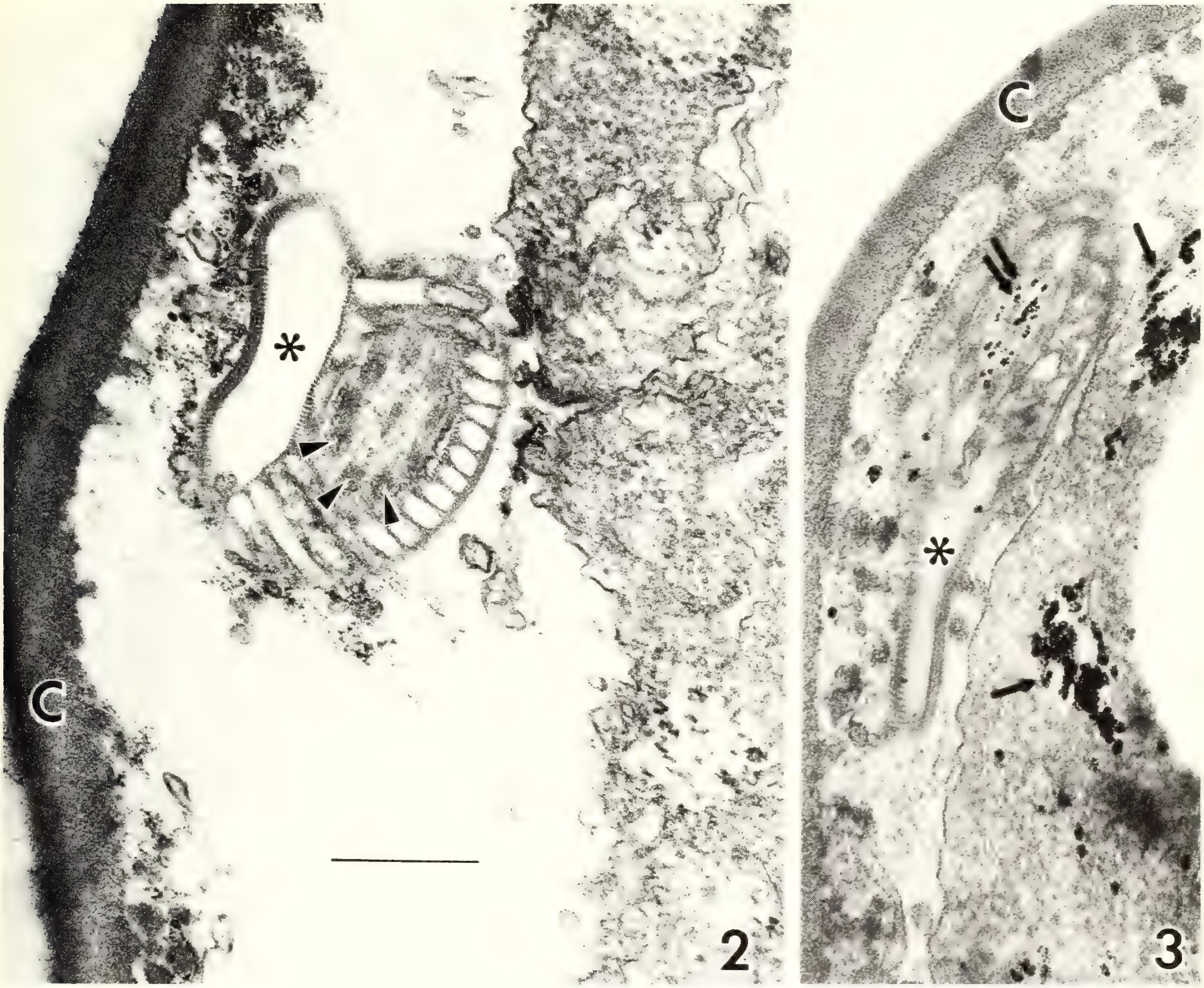
Regardless of the name applied to the organ that secretes the capsules, the egg capsule walls are believed to be formed of neutral mucopolysaccharide in the following manner (based on Ghiselin, 1965). The capsule material is secreted as droplets that will form a thin sheet around the eggs. As the eggs and sheet are rotated by cilia, the sheet surrounds the eggs singly or in groups, depending on the species. Rotation continues and divides the egg covering into packets (individual capsules). Sometimes the locations where a capsule rotated apart from its neighbors are visible as twisted regions of the capsule wall, termed chalazae. The capsule is laid down on the egg (or egg and albumen) surface. The egg is said to then shrink, producing an intracapsular space.

CAPSULE CONTENTS AND POSSIBLE ADAPTIVE VALUE

The gelatinous matrix (= egg mass) surrounding nudibranch egg capsules might protect the developing embryos from infestation, predation, osmotic stress, desiccation stress, mechanical damage, or pollutant stress (Todd, 1981) but the adaptive value of embryonic capsules themselves has not been considered. We can perhaps approach this question by examining the capsule contents. When extruded from the reproductive system of the parent, each capsule typically encloses three things: egg(s), sperm, and intracapsular fluid that may contain albumen. Some capsules lack eggs but whether these capsules also lack sperm and/or albuminous fluid has not been determined. These so-called "empty capsules" are frequently smaller in diameter than egg-containing capsules and are typically located at the beginnings and ends of the egg mass strings or ribbons (Thompson, 1958).

Inside the capsule each fertilized egg either aborts or develops into an embryo. Unlike capsules of some prosobranch gastropods, those of nudibranchs do not serve to enclose nurse eggs; no nudibranchs provide nurse eggs as an extraembryonic food supply. In fact, many species typically have only one egg per capsule (Fig. 1) (Hurst, 1967). In a few nudibranch species, up to 60 eggs can be packaged within one capsule (Hurst, 1967). If an embryo aborts, the capsule physically isolates it from embryos other than capsule-mates; it is unknown if healthy embryos will feed on disintegrating capsule mates.

The capsule remains intact around the embryo for

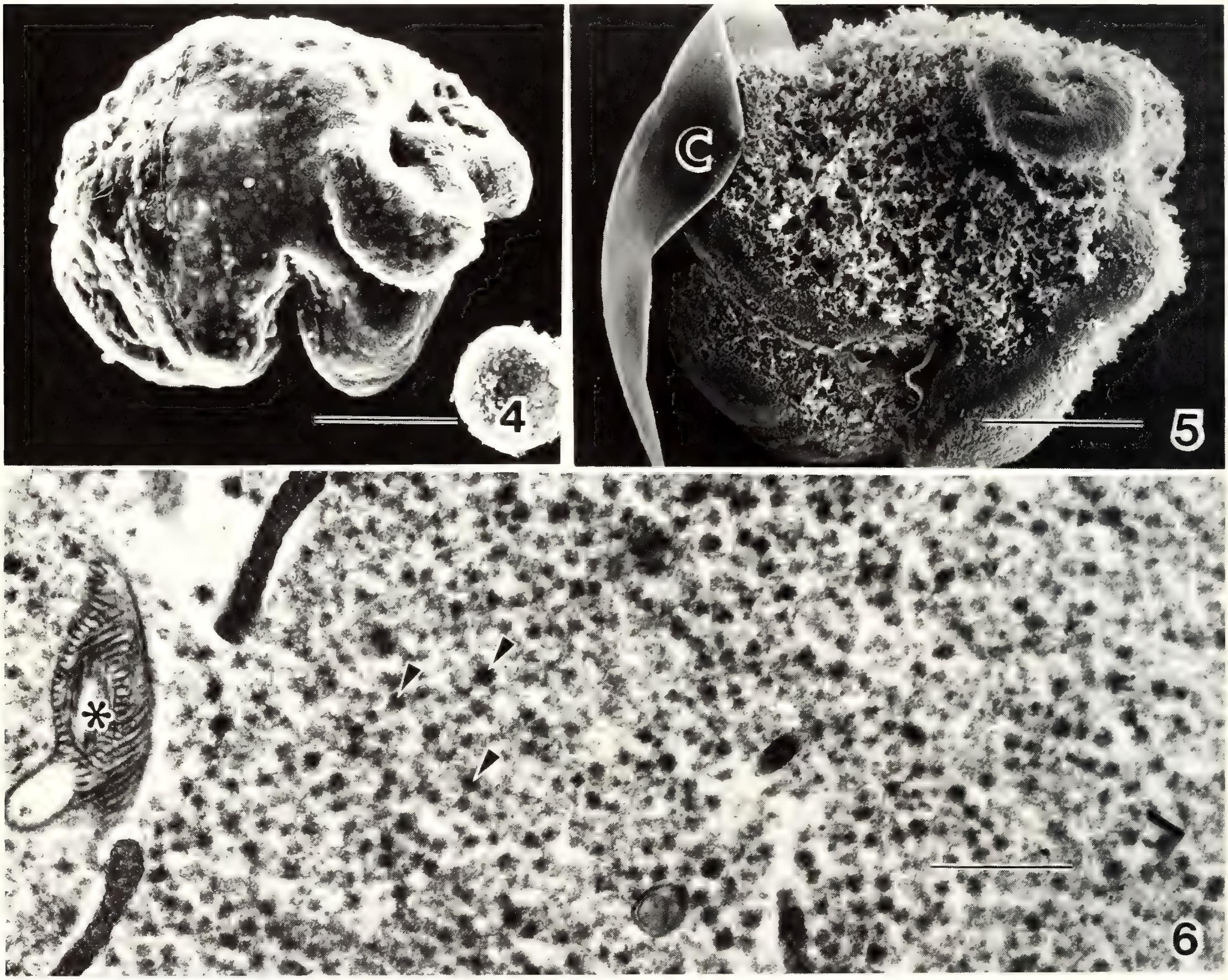


Figs. 2, 3. Transmission electron micrographs of sperm inside *Aeolidia papillosa* capsules (C) 14 days after capsule deposition. The 9 + 2 arrangement of microtubules (arrowheads) is still detectable, as is the periaxonemal sheath and keel (*). Glycogen is not detected in the lumen of the keel (*). **Fig. 2**. Standard TEM preparation followed by staining with uranyl acetate and lead citrate. **Fig. 3**. Standard TEM preparation followed by staining for periodate-reactive carbohydrates (arrows). Bar = 0.2 μm for both.

varying lengths of time from about 1-8 weeks depending on the temperature, the developmental pattern of the species, and various other factors associated with hatching. The organism that hatches from each capsule is either a free-swimming veliger larva or a crawling juvenile, depending on the species. Hatching is discussed below.

In addition to eggs, each capsule encloses multiple sperm (Figs. 2, 3). In nudibranchs, fertilization usually occurs inside the parent soon after gamete mixing (Schemekel, 1971). The fate of the supernumerary sperm is unknown. In some species, such as *Archidoris pseudoargus*, intracapsular sperm are not detected after oviposition, presumably because they are somehow readily degraded (Thompson, 1976). In other species they are visible and are capable of occasional movement several days after oviposition (Thompson, 1976; pers. observ.) In transmission electron microscopy (TEM) sections, sperm are occasionally observed fortuitously (Figs. 2, 3, 6). The sperm were visible with light microscopy within the capsules of *Tritonia hombergi* up to 14 days after oviposition (Thompson, 1976) and were detectable with TEM in *Coryphella salmonacea* capsules 50 days after oviposition (Fig. 6). The energy reserve of the sperm, glycogen-like particles in the helical keel (Anderson and Personne, 1976; Eckelbarger and Eyster, 1981), were not detected in *Aeolidia papillosa* sperm at 14 days (5°C) after oviposition (Figs. 2, 3) or in *Coryphella salmonacea* sperm at 50 days (5-8°C) after oviposition (Fig. 6). In one section subjected to PA-TSC-SP (periodic acid, thiosemicarbazide, silver proteinate) staining for carbohydrates (Thiéry, 1967; Porter and Rivera, 1979), material associated with the microtubules was periodate reactive (Fig. 3). Little to no periodate reactive substances were detected in the sperm keel (Fig. 3). These observations indicate that the sperm did not decay although their glycogen (energy) supply was apparently exhausted.

The third and last internal component of the capsule is the fluid (and sometimes particulates) lying between the developing embryo and the inner surface of the capsule wall. As the embryo develops cilia, it moves freely within this fluid. In some species the untreated fluid is reported to look granular rather than clear and it is this granular material that is sometimes referred to as albumen. We do not know if untreated albumen is always granular in appearance or how the presence of albumen varies with taxon, development type, or egg diameter. For sacoglossan opisthobranchs, Clark and Jensen (1981) reported three types of albumen: fine granular albumen (< 1 μm diam.), frothy (= alveolar) albumen, and vesicular albumen (up to 10 μm diam., usually attached to inner capsule wall). In the opisthobranch *Phyllaplysia taylori*, Bridges (1972) reported the presence of a large intracapsular body (49 μm diam.) that she believed was food for the embryo. In this paper I will use the term albumen to refer to any condensed, granular material, regardless of its chemical composition, observed with TEM or SEM, between the embryonic surface and the capsule wall.



Figs. 4-6. Electron micrographs of intracapsular albumen in the aeolid nudibranch *Coryphella salmonacea*. **Fig. 4.** SEM of 3½ week old embryo fixed and dried after manual excapsulation. Albumen was washed away from the embryonic surface. Bar = 100 μm. **Fig. 5.** SEM of 7 week old embryo fixed and dried while still inside intact capsule. An obvious layer of flocculent albumen precipitated from the intracapsular fluid is observed on the embryonic surface after the capsule (C) is broken away. Bar = 100 μm. **Fig. 6.** TEM of material lying between surface of 7 week old embryo and inner wall of intact capsule. The abundant granular material (arrowheads) is believed to be albumen. One sperm cross-section is shown at left (*). Bar = 1.0 μm.

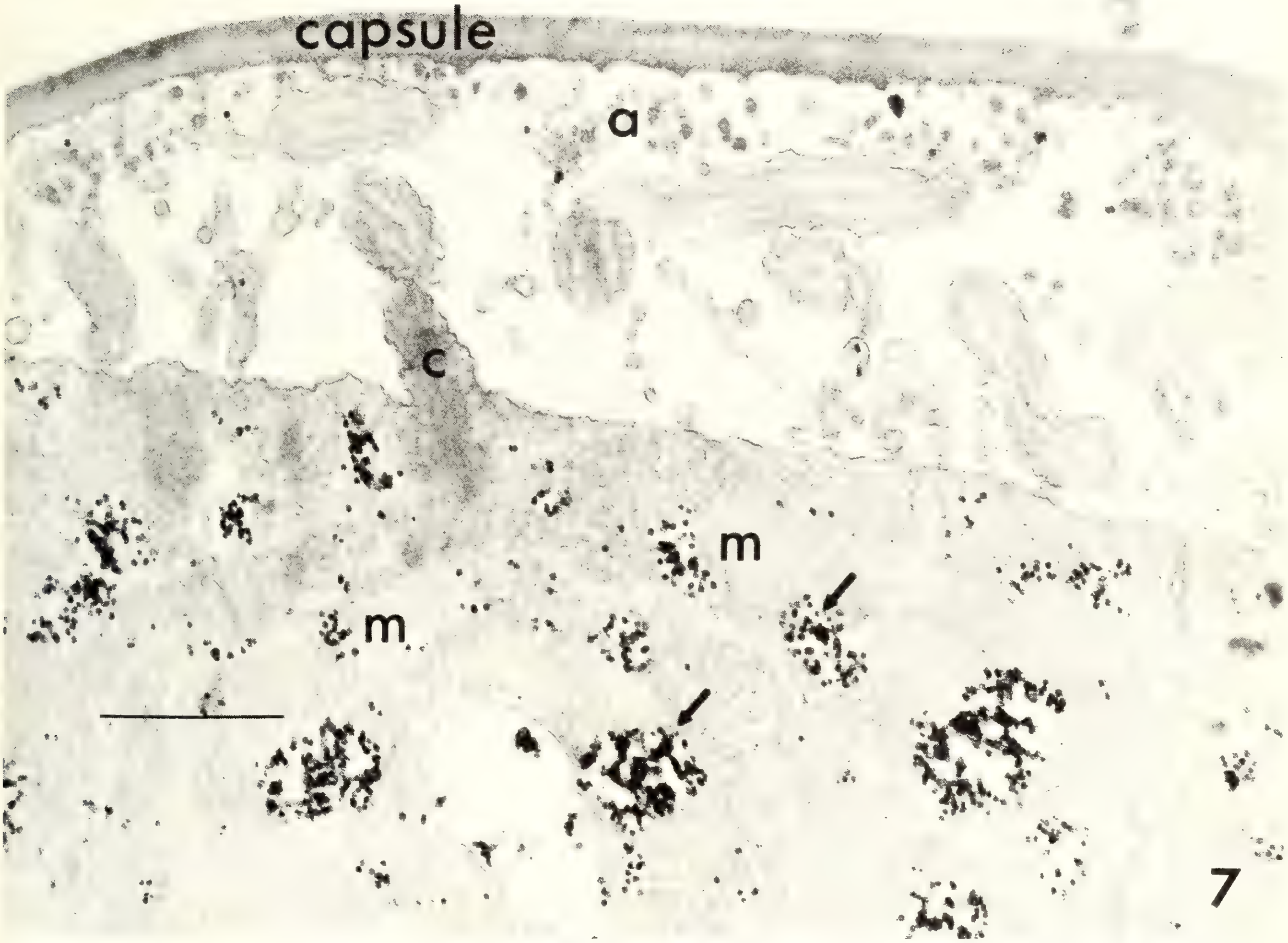


Fig. 7. Transmission electron micrograph of 14 day old *Aeolidia papillosa* (5°C) preveliger embryo in intact capsule. Neither the capsule wall nor the albumen (a) appear to contain carbohydrates oxidizable with periodic acid. The glycogen (arrows), which reacted with the periodic acid, appears electron dense. C = cilium. M = mitochondrion. Bar = 0.5 μm.

Aeolid nudibranchs are said to lack albumen (Ghiselin, 1965; Beeman, 1977). However, Kuzirian (1973) observed "albumen" in three coryphellid species and in the present study a granular substance presumed to be albumen was detected in the intracapsular fluid of three aeolids: *Coryphella salmonacea* (Figs. 4-6), *Aeolidia papillosa* (Fig. 7), and *Hermissenda crassicornis* (Fig. 10). With TEM, the precipitated material appears as electron dense granular material after exposure to glutaraldehyde, osmium tetroxide, uranyl acetate and lead citrate (Fig. 6). Clark *et al.*, (1979) have reported similar condensation upon fixation for albumen of the sacoglossan opisthobranch *Elysia cauze*.

The identification of this presumed albuminous material is not always certain. Although Kuzirian (1973) could detect albumen during passage of oocytes through the oviduct, once the capsule was fully formed, both the albumen and the capsule wall stained so similarly that it was impossible to histochemically distinguish the two with light microscopy. In many TEM sections in the present study it was difficult to ascertain whether some of the observed granular material is part of the movable intracapsular fluid or an integral part of the stationary capsule wall (Fig. 7). In the sacoglossan opisthobranch *Costasiella lilianae* the inner surface of the capsule wall is apparently lined with vesicles that are considered albumen and that break off and are consumed by the growing embryo (Clark and Goetzfried, 1978); the prevalence of this mode of potential embryonic nutrition among opisthobranchs is unknown.

The composition of the intracapsular fluid and particulates of nudibranchs has been examined histochemically by Ghiselin (1965) and Kuzirian (1973). Ghiselin (1965) concluded that albumen was lacking in the aeolid *Hermissenda crassicornis*, and was composed of neutral carbohydrate in the dorid *Dendrodoris albopunctata*. Kuzirian (1973), in contrast, determined that albumen was present in three *Coryphella* (Aeolidacea) species and was a weakly acidic sulfated mucopolysaccharide. Bayne (1968) histochemically identified both carbohydrate and protein in the intracapsular fluid of the opisthobranch *Aplysia punctata*. In the present study preliminary tests with the PA-TSC-SP stain for periodate-reactive carbohydrates (Thiéry, 1967; Porter and Rivera, 1979) indicated that no carbohydrates oxidizable with periodic acid were detected in the intracapsular fluid of 14 day old (5°C) pre-veliger *Aeolidia papillosa* (Fig. 7). More studies of the chemical composition of the intracapsular fluid may aid our understanding of its possible role or adaptive value.

How might the intracapsular albuminous fluid function? The fluid inside the capsule probably influences diffusional exchange of gases for respiration and of wastes. Although the albumen is often said to be nutritive (e.g. Ghiselin, 1965; Beeman, 1977) there is no convincing evidence that it is. The observation that the perceived granularity sometimes disappears during development is used as evidence that the intracapsular material of nudibranchs is nutritive. However, the granular material may disappear through solubilization rather than through ingestion. Kuzirian (1973) believed that the thin albumen layer observed in capsules of three aeolid nudibranchs served no important nutritional role but rather formed the first mucus layer around the eggs. It would be near impossible to determine the caloric content of the intracapsular fluid from such tiny capsules; the caloric content or dry weight of the capsule and albumen are usually lumped together with that of the intact egg mass (e.g., DeFreese and Clark, 1983; Smith and Sebens, 1983).

To examine the fate of the albuminous material during embryonic development, encapsulated embryos of the aeolid *Coryphella salmonacea* were examined with TEM (by standard techniques; Eyster, 1983) to determine when the albumen disappeared if at all and if there was evidence of albumen uptake by the embryo. All capsules were fixed intact to avoid possible leakage of capsular fluid contents. Intracapsular fluid from 1, 2, 4, 6, and 7 week old capsules (maintained at 5-8°C) all contained abundant albumen. Significantly, albumen was still abundant in capsules from which the young nudibranchs were ready to hatch (Fig. 6). (Hatching readiness was determined by active hatching from adjacent capsules in the same region of the same egg mass). Unless the albumen is consumed immediately upon hatching, this evidence suggests that the albumen does not serve a major nutritive function in this species.

Similar and more detailed studies should be conducted with other species to answer some of the following questions: What is the composition of the intracapsular fluid? Does the composition change during development? Does the albumen ever bind to or derive from the capsule wall? Is any or all of the material ingested? If it is ingested, is it assimilated? Is there evidence of pinocytotic uptake?

For sacoglossan opisthobranchs Clark and Jensen (1981) were able to demonstrate the nutritive importance of albumen by observing prolonged intracapsular development associated with presence of albumen. In another sacoglossan, a different, non-nutritive role has been suggested for the albumen. Chia (1971) suggested that the granular albuminous material inside capsules of the sacoglossan *Acteonia cocksi* was a dehydrated substance serving to expand the capsules via hydration, resulting in increased space for the developing embryos. If this is true for sacoglossans it may also be true for those nudibranchs in which the capsules enlarge as the embryos develop. Kress (1971, 1972) reported that distinct increases in capsular volume occurred in some nudibranch species when the velar cilia developed, perhaps due to uptake or modification of some capsular fluid component or to excretion of wastes. If the albuminous material is to hydrate, it must alter chemically and/or additional water must enter the capsule from outside. This influx of water could follow a change in capsule permeability to water or an increase in internal osmotic concentration. Not all sacoglossans have capsule enlargement (Chia, 1971; Kress, 1971, 1972) and among nudibranchs degree of enlargment varies among species (Kress, 1971, 1972, 1975). A study correlating presence/absence of albumen and capsule enlargement has not been undertaken. It may also be informative to determine if changes in capsule volume are accompanied by changes in capsule fluid histochemistry. If albumen is present in so-called "empty" capsules and if these capsules do not enlarge when neighboring embryo-containing capsules do, we may conclude either that the albumen is not involved in capsule enlargement or that presence of an embryo alters the albumen.

CAPSULE PERMEABILITY

Strathmann and Chaffee (1984) have recently discussed factors that are likely to influence oxygen diffusion through gelatinous egg masses such as those of opisthobranchs; however, the permeability of nudibranch capsules and egg masses to oxygen, water, metabolic wastes, dissolved nutrients, and salts is an unexplored subject. Some preliminary data on capsule permeability and the effects of enzymes on permeability and puncturability are therefore presented below. During a study of *Coryphella salmonacea* embryonic shell formation (Eyster, 1985) I observed that embryos within broken capsules sectioned better than those with intact walls. The intact capsule apparently inhibited passage of fixatives and/or embedding media through the capsule wall. This was true throughout prehatch development, indicating that capsule permeability to the fixative did not increase with age. Because of poor penetration of fixatives and/or embedding media through the capsule wall, I explored methods of removing the capsule from around the embryo or of altering capsule permeability prior to fixation. The egg capsules usually were easily dissected from the gelatinous egg mass in this species. Manual removal of the 350 x 430 μm diameter capsules without damaging the embryos could be accomplished following micropuncture of the capsule wall (see technique in Eyster, 1985) but was a difficult and tedious procedure. As the capsules are probably partly protein and partly carbohydrate (Ghiselin, 1965; Bayne, 1968; Kuzirian, 1973), I tried improving capsule permeability by briefly incubating intact capsules in enzymes (Table 1, including two proteolytic enzymes and three which act on carbohydrates) prior to standard TEM fixation. Capsules were removed from the

Table 1. Enzymes (0.1 mg/ml) used to pretreat intact 15 day old *Coryphella salmonacea* capsules prior to preparation for transmission electron microscopy. (+ = yes; - = no; ± = result inconsistent; blank = not tested) N = 3 or more capsules for each.

Enzyme	Treatment Time (min.)	Improved sectioning quality?	Increased puncturability?
trypsin	15	-	-
	45	-	±
protease	15	-	-
	45		±
α-amylase	2	-	-
	10		-
	20		+[1]
hyaluronidase	1		-
	4		-
	10		-
	30		-
	60	±	±
amyloglucosidase	2		-
	4		-
	6		-
	8	±	±
	10	±	-
	30	±	-
	45	±	

[1] Although capsule puncturability was improved, the enclosed embryo disintegrated.

gelatinous egg mass and were incubated with each enzyme (0.1 mg/ml of seawater) from 2-60 minutes (Table 1). After incubation, some of the enzyme-treated and untreated capsules were prepared for TEM. In all cases, embryos in micropunctured, untreated capsules were better fixed and/or infiltrated than embryos within intact capsules that were enzyme treated up to one hour. Among the pretreatment enzymes, only hyaluronidase and amyloglucosidase produced any sectionable embryos and results varied among capsules within the same test.

Untreated capsules of *C. salmonacea* were too turgid to pinch with forceps or to easily puncture. Enzyme-treated capsules were poked and prodded with forceps and microprobes to determine if the enzyme pretreatment facilitated manual capsule removal. All of the enzymes seemed to alter capsule turgidity (or at least capsule puncturability) but results varied from capsule to capsule (Table 1). In another attempt to decrease the difficulty of manually removing *C. salmonacea* capsules by first decreasing capsule turgidity, I subjected 10 day old, intact embryonic capsules (maintained at 30 ppt) to increased salinities (34, 35, 42, and 76 ppt). The 76 ppt and 42 ppt salinities were prepared with Instant Ocean in distilled water; the other salinities were prepared by adding Instant Ocean to natural 30 ppt seawater. In 76 ppt salinity the capsules soon lost turgidity, and the embryos began to disintegrate within 15 minutes. This presumably reflects outward diffusion of water across the capsule walls from higher internal to lower external water concentration and a corresponding increase in intracapsular osmotic concentration. At 42 and 35 ppt the capsules also lost turgidity but without corresponding disintegration of the embryos. At 35 ppt, capsule turgidity decreased within five minutes, but at 34 ppt about 12 minutes were required before the capsule lost sufficient turgidity (= lost enough water) to be micropunctured. Capsules also lost turgidity and became puncturable for 1-2 minutes when placed in glutaraldehyde fixative (~1200 mosm). However, after a few minutes in the fixative they often unexplainably regained turgidity and could not be readily punctured.

Other data suggest that the capsule wall is also an effective barrier to the calcium chelator EGTA (ethylene-glycol-bis-N,N-tetraacetic acid). Shells of encapsulated veligers of the nudibranch *Dendronotus frondosus* remained birefringent after a 30 min. incubation in 10 mM EGTA, whereas shells of newly hatched veligers began to lose birefringence (= lose shell $CaCO_3$) within 3 min. (Eyster, 1986). Data such as these suggest that the capsule wall is an effective barrier to EGTA.

These preliminary data suggest that the capsule walls of *Coryphella salmonacea* are permeable to water but not readily permeable to larger molecules such as those of salts, fixatives, and embedding media. Since the osmotic concentration apparently increased inside the treated capsules as water moved out, "albumen" probably did not exit through the walls. The ability to retain intracapsular albumen in the face of environmental salinity change may be important to the embryos if albumen contributes to successful development. Clark *et al.* (1979) reported the presence of an extracapsular yolk string that disappears during embryonic development in the sacoglossan *Elysia cauze* and suggested that embryonic enzymes might exit the capsule and dissolve this yolk, which then diffuses into the capsule. Clark has since stated he no longer thinks the yolk can pass into the capsule through the wall (Hadfield and Switzer-Dunlap, 1984).

PREDATION AND CAPSULE CONSUMPTION

Feeding on nudibranch egg capsules and masses is poorly documented. Fish have been observed to ingest nudibranch egg masses but it is not clear that the fish seek the egg masses as a natural food source. In the laboratory, I have observed adult *Coryphella salmonacea* and *Armina tigrina* feeding on their own egg masses, but this may be a sign of hunger rather than of natural dietary preference. There are several opisthobranch species reported to naturally feed on the egg masses of other opisthobranch species (Crane, 1971; Haefelfinger, 1962, cited by Gascoigne and Sigurdson, 1977). Chia (1971) observed that *Acteonia cocksi* (Sacoglossa) fed on their own egg capsules after hatching from them.

HATCHING

Although the method of hatching has not been demonstrated for any nudibranch, possible mechanisms of capsule rupture/breakdown (resulting in hatching) include enzymatic degradation, osmotic rupture, physical activity of the embryo, and degradation by bacteria and protists (Hurst, 1967; Harris, 1975; Davis, 1981; Todd, 1981). If hatching is a developmentally programmed event, then salinity and temperature will affect onset of hatching by altering rate of embryonic development, but there is no evidence that changes in either of these factors normally stimulate hatching in nudibranchs.

Hatching can be artificially delayed in the laboratory by maintaining egg masses in static culture (no aeration, change of filtered seawater and dishes daily) rather than in flowing seawater (Hurst, 1967; Harris, 1975; Rivest, 1978; Eyster, 1979, 1985). For example, I collected pairs of egg masses laid on the same day in the laboratory by *Aeolidia papillosa, Tenellia pallida,* or *Coryphella salmonacea* and divided them between flow-through and static culture conditions. The egg masses placed in flowing seawater hatched before the masses kept in static culture. Embryos in static culture often rotated in their capsules more slowly. If egg masses in static culture were then aerated or transferred to fresh seawater, the young nudibranchs increased their activity rate and soon hatched. These observations suggest several possibilities: 1) Flowing water may provide more oxygen to the developing embryos. In static culture low intracapsular oxygen concentrations may evolve and inhibit development. 2) Flowing water may increase rate of diffusion of embryonic wastes out of the capsules. Waste build-up in static culture may inhibit embryonic development and embryonic activity. 3) Transfer of newly laid egg masses to clean dishes and filtered seawater may decrease abundance on/in egg masses of bacteria, which have been implicated in promoting nudibranch hatching (Harris, 1975). These three possibilities could be tested in the laboratory by controlling water flow, dissolved oxygen levels, and bacterial abundance.

Hatching may involve more than one mechanism. Even if nudibranch embryos do not produce hatching enzymes, the capsule wall may be altered during development in response to increased intracapsular osmotic pressure. As mentioned above, Kress (1971, 1972) has demonstrated that the capsules of some nudibranch species swell during development. Although the capsules may swell during development, they seem to lose their normal turgidity just prior to exit of the embryo and are readily deformable even by the pressure of velar cilia (Thompson, 1958; Perron and Turner, 1977; pers. obs.). Nudibranch capsules do not seem to burst open and then shrink like punctured balloons because the capsule walls are not as elastic. After hatching the capsules are typically flaccid. The hatching mechanism may be different for the antarctic *Austrodoris macmurdensis*, which is reported to have unusual chitin-reinforced capsules that are tightly abutted in a beehive-like arrangement (Gibson, *et al.*, 1970). Hatching was effected through ruptures in the uncollapsed capsule wall.

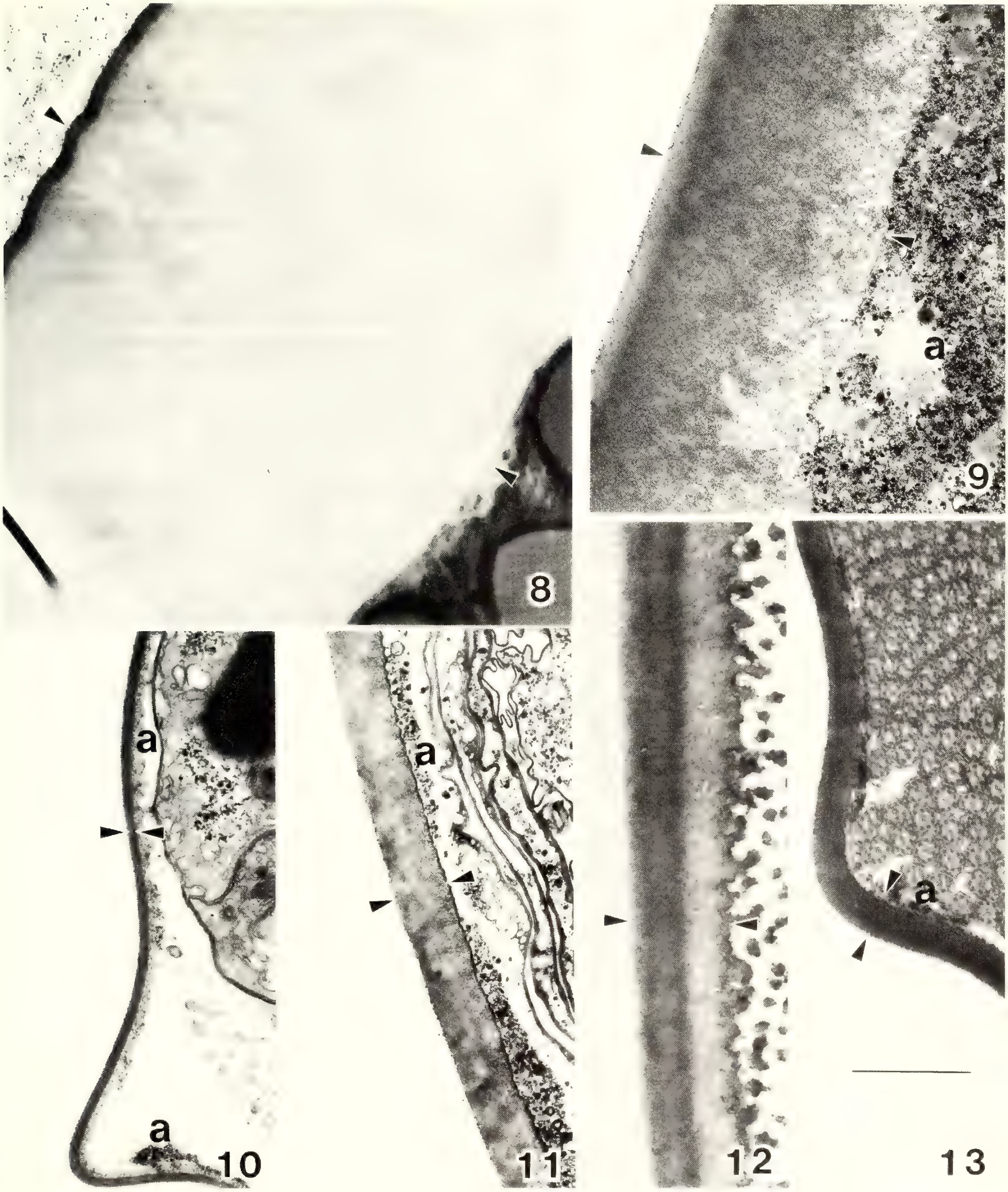
If a capsule increases in diameter during development, it must simultaneously decrease in wall thickness, unless new wall material can be added from the intracapsular fluid/albumen. There is no reason to believe that embryonic secretions are added to the wall and there is no ultrastructural evidence of preformed capsule wall indentations that could allow for capsule expansion. Although neither change in capsule thickness over time nor binding of albumen to the capsule wall have been demonstrated to occur, the former (decreased capsule wall thickness) might ease mechanical or chemical hatching for the embryo, and might provide less of a barrier against bacterial and protozoan invaders. A thinner capsule wall may also be more permeable to oxygen and wastes. Studies of capsule wall structure and permeability from deposition to hatching might provide some clues to how nudibranch embryos hatch.

CAPSULE ULTRASTRUCTURE

Most nudibranch capsules are so thin that transmission electron microscopy is needed to examine their structure. For the present study, capsule ultrastructure is shown for six species (Figs. 7-13). All capsules were obtained from egg masses deposited in the laboratory. Adults were obtained from the following locations: *Archidoris montereyensis* (Friday Harbor, WA); *Cadlina laevis* (Shoals Marine Laboratory, ME); *Hermissenda crassicornis* (courtesy of June Harrigan, Woods Hole, MA, from Californian adults); *Coryphella salmonacea* and *Aeolidia papillosa* (Nahant, MA); *Dendronotus frondosus* (Eastport, ME).

For five of the six species some capsules were fixed when the enclosed embryos were trochophores. Random additional capsules were also fixed. All capsules contained one healthy individual, except for those of *Aeolidia papillosa*, which contained three. For the two dorids, only one egg mass each was available. For *Dendronotus frondosus* capsules from two different egg masses at different stages of development were used (half-shelled veliger stage, fully-shelled veliger stage). For two of the aeolid species, capsules were examined from at least two egg masses from different parents and/or from two stages of development (over time) from the same egg mass. For the third aeolid (*Aeolidia papillosa*) I examined capsules from a single egg mass, fixed at four times over a single day (312, 315, 325, 335 h after oviposition).

For each species the egg mass matrix was teased open and capsules were removed and pipetted into the fixative. Following glutaraldehyde-osmium tetroxide fixation and uranyl acetate—lead citrate staining (Eyster, 1983), the capsule walls of all species examined were at least moderately electron dense and in most species did not exhibit any consistent distinct layers. In the few available sections of *Archidoris montereyensis* capsules the outermost portion ($\sim 0.1 \mu m$ wide) of the capsule was distinctly more electron dense but not obviously different in texture from the rest of the capsule (Fig. 8). This narrow outer zone of the capsule was as wide as the total capsule wall of *Aeolidia papillosa* (Fig. 7) or of *Hermissenda crassicornis* (Fig. 10). The other striations seen in the *A. montereyensis* capsule micrographs (Fig. 8) are artifacts from damage to the knife edge by what appeared to be diatoms and small sand-like particles stuck to the jelly mass surrounding the capsules. In this particular species the capsules were not easily separable from the



Figs. 8-13. Transmission electron micrographs of capsule walls from five nudibranch species, all shown at the same final magnification. The outer surface of the capsule is towards the left for each figure, and the width of each capsule wall is demarcated with arrowheads. Fibrous material, believed to be part of the gelatinous egg mass, is seen on the outer capsule wall in Figures 8, 12 and (faintly) 13. **Fig. 8.** *Archidoris montereyensis,* about 5 d old, just prior to onset of embryonic movement. **Fig. 9.** *Cadlina laevis,* mid-veliger stage, age unknown. **Fig. 10.** *Hermissenda crassicornis,* age unknown, embryo shelled. **Figs. 11-12.** *Coryphella salmonacea,* 6 wk. and 4 wk. old veliger stages respectively, from different masses. **Fig. 13.** *Dendronotus frondosus,* fully shelled veliger stage, age unknown. A = granular material presumed to be albumen, present in the intracapsular space. Bar = 0.5 μm for all.

gelatinous egg mass, a portion of which is visible as scattered fibers on the outer capsule surface (Fig. 8, upper left). In other species, debris did not interfere with sectioning either because the capsules were easily separable from the gelatinous mass or because the jelly did not bind debris as readily.

Capsule morphology for each species was relatively consistent under the conditions used except for *Coryphella salmonacea*. In *C. salmonacea* the capsule wall in some sections was unlayered (Fig. 11); in other sections of capsules from a second mass the wall seemed layered, the outer part being of comparable width and texture but of greater electron density than the inner part (Fig. 12). Why the capsules of this one species sometimes but not always appeared layered is unclear. The influence of fixative contents, fixative osmotic concentration, and developmental stage on capsule morphology have yet to be determined.

Besides the fibrous material on the outer surface of some capsules (Figs. 8, 12, and 13), which is believed to be part of the gelatinous egg mass, some capsules of *Aeolidia papillosa* (Figs. 2, 7) and *Coryphella salmonacea* (Fig. 12) seemed to have projections on the inner capsule surface. However, the distinction between apparent capsule wall projections and intracapsular albuminous materials was often obscure. These projections did not appear to be a layer of vesicles as described by Clark and Goetzfried (1978) for a sacoglossan opisthobranch *Costasiella lilianae*. The inner capsule wall of other examined species was smooth.

Capsule wall thickness in the six species examined varied from a minimum of 0.07 μm in *Hermissenda crassicornis* (Fig. 10) to a maximum of 4.5 μm in *Archidoris montereyensis* (Fig. 8). Because apparent capsule wall thickness can vary with sectioning angle, the average observed thickness (not the maximum thickness resulting from oblique sectioning angle) was recorded (Table 2). Based on the few available data for the six species examined, capsule wall thickness was not obviously correlated with developmental type, days to hatching, or number of embryos per capsule (Table 2). There may be better correlations between characteristics of the gelatinous mass (thickness, durability) and developmental type or hatching time (Todd, 1981).

The thickest capsules occurred in members of the Doridacea but more species need to be examined to determine if dorids typically have thicker-walled capsules. Both thin walled and thick walled capsules surrounded embryos that would develop into planktotrophic larvae. For species with multiple embryos per capsule, more detailed study of capsule wall thickness is required to determine if capsule wall material stretches (is thinner) around larger groups of embryos or if a larger capsule of the same thickness is produced. The relationship between capsule wall thickness and prehatch developmental time is more problematical because hatching time is so temperature sensitive and because the six species examined were not reared at the same temperature (Table 2). Some species with shorter prehatch developmental periods had thinner capsules (e.g. *H. crassicornis*), yet one species with prolonged development (*C. laevis*) had a capsule of medium thickness and another species of medium hatching time had the thickest capsule wall (*A. montereyensis*).

SUMMARY

This paper reviews our knowledge of the origin, contents, adaptive value, composition, hatching, and structure of the embryonic capsules of nudibranch molluscs. Most comments in this paper probably also apply to other opisthobranch gastropods that produce small capsules within a gelatinous egg mass. Our knowledge is minimal and there are many areas of study left to be explored. We know the capsules are secreted by the parental reproductive system but it is unclear where and how the capsule wall and

Table 2. Comparison of embryonic capsule wall thickness with taxon, development type, approximate time to hatching, and number of eggs per capsule for six nudibranch species.

Species	Suborder	Development Type	Days to Hatching*	Eggs/ Capsule	Observed Capsule Wall Thickness
Archidoris montereyensis	Doridacea	Planktotrophic	20-24 @17°C[1] 23-28 @8-11°C	1-3	4.0–4.5 μm
Cadlina laevis	Doridacea	Non-planktonic Lecithotrophic	50 @10°C[1]	1	1.7–2.0 μm
Dendronotus frondosus	Dendronotacea	Planktonic Lecithotrophic	6 @14°C[2] 7-15 @8-11°C 32 @10°C[1]	1	0.25–0.35 μm
Aeolidia papillosa	Aeolidacea	Planktotrophic	10-24 @8-11°C	3-19	0.10–0.17 μm
Coryphella salmonacea	Aeolidacea	Non-planktonic Lecithotrophic	25-34 @5-8.5°C[3] 56 @5°C[4]	1	0.5-1.2 μm
Hermissenda crassicornis	Aeolidacea	Planktotrophic	7-8 @8-11°C 5-6 @ 13-15°C[5]	1-4	0.07–0.11 μm

*from Hurst, 1967, unless otherwise specified

[1]Thompson, 1967; [2]Williams, 1972; [3]Morse, 1971; [4]Eyster, 1985; [5]Harrigan and Alkon, 1978.

intracapsular fluid are secreted. Some species are known to have an intracapsular albuminous substance. The taxonomic distribution and chemical composition of this substance are still matters of debate. The capsules of nudibranchs are probably composed of some combination of carbohydrates and proteins, although proportions of carbohydrate to protein and actual composition may vary with species and even with time. The capsule walls are all thin, but vary in thickness from 0.1 to 4.5 μm in those species examined. Based on the few data available, capsule wall thickness is not obviously related to suborder, developmental type, hatching time, or number of embryos per capsule. The mechanisms by which nudibranch embryos manage to exit their capsules may include enzymatic, osmotic, and/or mechanical means, but all of these remain to be demonstrated. The proposed adaptive value of capsules and the surrounding gelatinous matrix is that they protect the developing embryos from infestation, predation, osmotic stress, desiccation stress, mechanical damage, and pollutant stress. Although some of these possible functions have been examined for prosobranch gastropods, none have been experimentally tested for opisthobranch gastropods.

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ENCAPSULATION OF CEPHALOPOD EMBRYOS: A SEARCH FOR FUNCTIONAL CORRELATIONS

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ABSTRACT

This article considers basic traits and group-typical modifications of egg encapsulation in the molluscan class Cephalopoda, emphasizing evolutionary aspects of the coordinated organization of capsule production by the adult and structural adaptation of the embryo, especially with regard to hatching mechanisms. Particular attention is given to the modifications observed in octopods, in which nidamental glands lying outside the terminal oviduct are lacking. All material secreted around the egg chorion (cirrate octopods) or chorion stalk (incirrate octopods) is produced by the complex oviducal gland, which thus fulfills the function of both oviducal and nidamental glands of decapods. The incirrate octopods are unique in that the protective function of encapsulation is entirely replaced by the active protection of naked eggs by the female (brooding or ovovivipary).

Encapsulation of eggs appears to be a basic means of protecting developing embryos in the class Cephalopoda. The presence of a large nidamental gland complex in *Nautilus*, the only living representative of the ectocochlean cephalopods, and its positional, structural and supposed functional similarity to endocochlean (coleoid) nidamental glands indeed suggest that encapsulation of eggs is a common ancestral character of the class.

Within the coleoid cephalopods, there are various modifications in capsule structure, although these capsules are produced by a largely uniform apparatus of capsule formation. Evidently these modifications reflect adaptive "strategies" responding to extrinsic (ecological) and intrinsic (development *s.l.*) constraints. They can be viewed in the evolutionary context of coordinated organisation (i.e. intrasystemic coadaptation of functional components). Although many gaps in our knowledge of encapsulation of cephalopod eggs remain to be filled, the available data already permit a framework of questions to be raised in approaching functional correlations within the mechanism of encapsulation. This brief survey attempts to outline the subject using data available in the literature and unpublished observations.

As with many other areas of cephalopod research, an historical résumé of published observations could start out with the written report (on the eggs and their capsules) given by Aristotle. Here it is sufficient to recall the thorough analysis of encapsulation in decapods (orders Sepioidea and Teuthoidea) published by Jecklin (1934) with a careful survey of the older literature. Jecklin provides a detailed description of the structure of the mucinous egg cases in cuttlefish, sepiolid and teuthoid squids, analyzes the changes they undergo during embryonic development, and finally studies hatching mechanisms. More recent data are reviewed in vol. IV of "Reproduction of marine invertebrates" edited by Giese and Pearse (1977), in both volumes of "Cephalopod Life Cycles" edited by Boyle (1983, 1986), and in vol. VII of "The Mollusca" (Reproduction) edited by Tompa, Verdonk and van den Biggelaar (1984) where cephalopods (Arnold, 1984) are reviewed along with gastropods and bivalves.

ORGANS PRODUCING CAPSULE MATERIAL

The mature cephalopod ovum (ovarian egg) is surrounded by the chorion, a product of the follicular cells. Although in chronological terms this is the primary egg cover, it is generally called the secondary envelope; the fertilization membrane (vitelline membrane), which forms a temporary cover of the embryo at early developmental stages, is termed the primary envelope. All additional material added to the outside of the chorion may be called tertiary envelopes. It is indeed of little use to call the more or less distinct outer coat or shell quaternary, as it is not distinguishable by its mode of production. Within the so-called jelly coats lying inside the outer coat, there are again two different components laid sequentially, as shown by Jecklin (1934). Probably in all cephalopods, some jelly is produced by the distal part of the oviduct, which forms a more or less compact glandular ring both in paired (oegopsid squids, incirrate octopods) and unpaired, unilateral oviducts (*Nautilus,* cuttlefish, sepiolid and myopsid squids, cirrate octopods).

In *Nautilus* and in most of the decapods, a pair of nidamental glands lies in the mantle cavity, with their open-

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ings situated close to the oviducal outlet(s). Although the process of nidamental jelly release has so far not been observed *in situ*, it seems most likely that eggs leaving the oviduct are immediately enveloped by the mucinous material "flowing" out of the nidamental glands (Arnold and Williams-Arnold, 1977). Eggs leaving the oviduct intermittently, one by one, are apparently enveloped individually; eggs leaving the oviduct serially are enveloped in a capsule enclosing a series of eggs.

Whether the paired accessory nidamental gland regularly provides secretions (Arnold and Williams-Arnold, 1977), e.g. for the formation and/or hardening of an outer coat, is not yet clear. The presence of bacteria in the winding ducts of this organ (Bloodgood, 1977), and the presence of clustered bacteria in the outer coat of *Rossia* eggs (Boletzky and Boletzky, 1973) suggest that the accessory nidamental gland may have a more complex role in the physiology of encapsulation than merely a function of finishing the capsule surface, but nothing is really known.

Finally it has been suggested that the salivary glands also contribute to the finishing of capsular structures (Jecklin, 1934). Similar suggestions concerning an intervention of salivary gland secretions in egg string formation by *Octopus* females are summarized by Prezant (1985) who quotes from earlier papers (Wood, 1963, Gennaro *et al*., 1965). However, the oviducal gland secretion of octopus females provides most, if not all, of the "cement" material for the chorion stalks typical of the eggs of incirrate octopods (Froesch and Marthy, 1975). This oviducal gland secretion corresponds to the capsule material forming the outer envelope of cirrate eggs (Boletzky, 1978-79, 1982a). The complex structure of the octopodan oviducal gland, and in particular of the clearly bipartite gland of cirrate octopods (Meyer, 1907, Aldred *et al*., 1983) ultimately raises the evolutionary question of the developmental pathways of structural modifications concerning both nidamental and oviducal glands (see Discussion). Here it can only be stated that the oviducal gland of cirrate octopods does indeed produce capsule material forming an envelope very similar to certain decapodan egg capsules, especially to those of *Rossia* eggs.

CAPSULE ARCHITECTURE IN DIFFERENT GROUPS

To use the term architecture of "slimy" secretions making up largely gelatinous coats that go through changes of size and structure during development of the embryos may appear inappropriate. However, in most instances, there is indeed a well-defined combination of volume, consistency and "packaging" in the secretory product that pre-programs the living conditions of the encapsulated embryos for the entire time of their development, which may last from a few days to more than one year depending upon species. In this section the capsule architectures typical of the different cephalopod groups are briefly described.

SUBCLASS NAUTILOIDEA

Nautilus eggs were described by several authors, beginning with Willey (1897). A peculiar feature of these very large eggs is that the hard outer coat is drawn out into a series of prominent folds each ending in an opening (cf. Haven, 1977). Thus the inner capsule only is entirely sealed from the outside. In preserved egg capsules I found the inner envelope to be continuous with the outer at the "attachments" described by Willey (1897). Thus the outer capsule appears to be an overturned bell-shaped ruffle, the edge of which is drawn over the apex of the inner capsule (leaving the resulting folds to form the open channels) before the egg is attached to the substratum.

As live observations of developing *Nautilus* embryos have become possible only very recently (Arnold and Carlson, 1986), it is too early to attempt functional interpretations of these structures, especially with regard to the hatching mechanism.

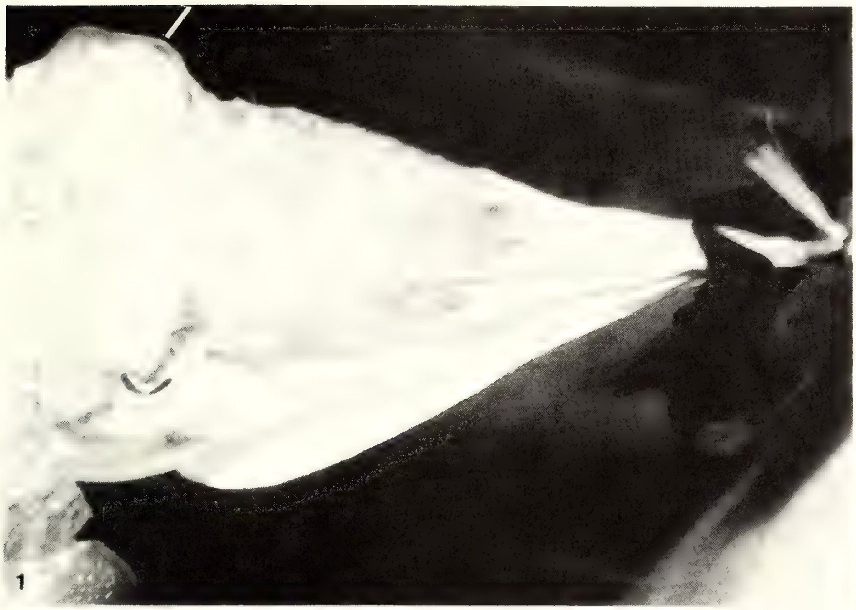
SUBCLASS COLEOIDEA

ORDER SEPIOIDEA

No observations are known on spawning in the pelagic genus *Spirula*. In the genus *Sepia*, the chorion of each egg is surrounded by spirally coiled oviducal jelly (Jecklin, 1934), plus a spirally coiled envelope of nidamental gland jelly, which in turn is surrounded by a soft outer coat (Figs. 2, 3). In *Sepia officinalis* Linnaeus, 1758, these envelopes are normally coloured by ink released with the jelly at spawning (Grimpe, 1926). At the moment of spawning, the female approaches an appropriate substrate for egg fixation, aims at the target site with binocular vision (Fig. 1), and at the same time uses the arm tips to draw out the very soft jelly coats into two filaments. Once she has made contact with the chosen substrate (any rod-like object or eggs already laid), she winds these filaments around the support so that they stick together and form a fixating ring. In aquaria, females unable to find an appropriate substrate for the fixation of their eggs drop them without producing filaments (for *Sepia orbignyana* and *S. elegans* see Ecological aspects of encapsulation).

The eggs of the Sepiolidae are rather similar to *Sepia* eggs, but they are always simply glued to a substrate, no matter whether it is flat or has prominent structures that would allow fixation by a ring. In the subfamily Sepiolinae, the outer coat is leathery and somewhat elastic (Fig. 6), whereas in *Rossia* eggs (and probably in the eggs of all Rossiinae), it is perfectly rigid. This outer case is ca. 200 μm thick (Fig. 5); it is made of several layers, which at the moment of laying are still very soft (Boletzky and Boletzky, 1973). Hardening into a true shell takes several hours. *Rossia* females space out their eggs on a substrate in regular intervals. When the egg capsules of this ground layer are firm, the spawning animal lays subsequent eggs on top of them. A typical egg mass of *Rossia* finally shows a fairly regular three-dimensional network, the eggs being piled up around large interstices (Fig. 4). They are most often found in empty bivalve shells (especially *Pinna pectinata* Linnaeus, 1767 in *Rossia macrosoma* [Delle Chiaje, 1829]), in which they are fixed to the ceiling of the shelter formed by the empty shell lying on the ground.

Sepiola and *Sepietta* eggs may also be laid in several layers, but they never form a loose three-dimensional network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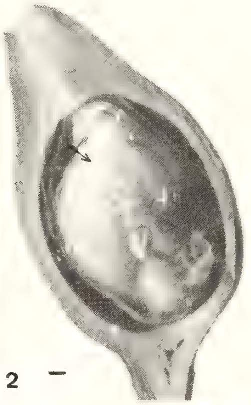
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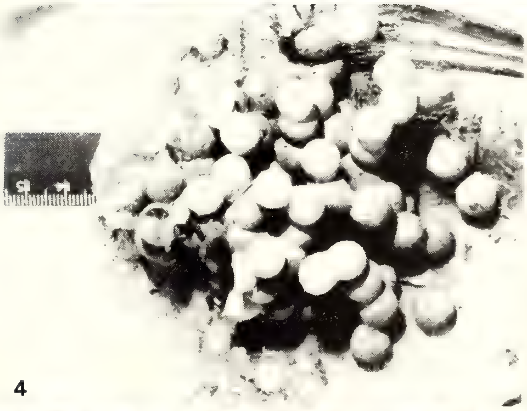
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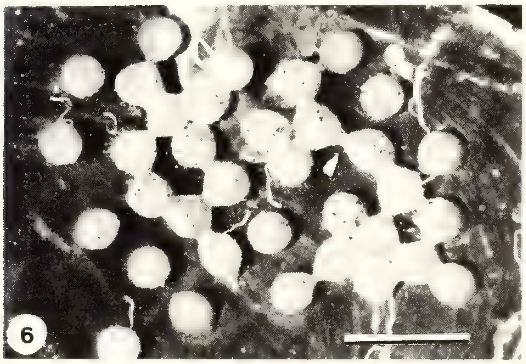
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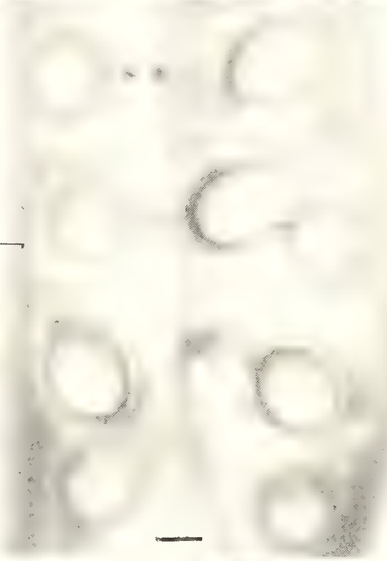

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Fig. 1. Female *Sepia officinalis* seen from the water surface while attaching an egg to a shackle suspended in the tank. The two bars indicate the middle axis of the eye ball to show convergent orientation for binocular vision; note also the arm tips stretched out towards the egg support. **Fig. 2.** An egg envelope of *Sepia officinalis* (laid empty, without an ovum), cut open. Inside the shrunken outer envelopes, the cavity normally containing the ovum is filled with a spirally coiled sheet of softer jelly, probably corresponding to the coiled oviducal jelly described by Jecklin (1934). Arrow indicates area enlarged in Fig. 3. Scale bar = 1 mm. **Fig. 3.** Detail of Fig. 2 at higher magnification. **Fig. 4.** Egg mass of *Rossia macrosoma* on a *Pinna pectinata* shell. **Fig. 5.** Semithin section through the outer shell of an egg of *Rossia macrosoma*. Note the very dense layers at the surface (above) and the alveolated inner layer (below). Scale bar = 10 μm. **Fig. 6.** Eggs of *Sepiola* sp. on a *Pinna* shell. Arrow head points to an elongated junction (see text). Scale bar = 10 mm. **Fig. 7.** Egg capsule of *Loligo vulgaris* shortly after laying, showing the spiral arrangement of the string of eggs embedded in oviducal jelly. Note the inversion of coiling direction in the lower right (this is close to the end of the capsule). Scale bar = 1 mm. **Fig. 8.** Enlargement of the area indicated in Fig. 7, after removal of the outer coat.

like egg masses of *Rossia*. As a consequence, the embryonic development of eggs covered by others is slowed due to poor oxygenation (Boletzky, 1983, Bergström and Summers, 1983).

The eggs of *Idiosepius*, the pygmy cuttlefish of the Indo-Pacific, are rather similar to the eggs of Sepiolinae, but there seems to be no distinct outer coat (Natsukari, 1970).

At the moment of laying, the spirally coiled nidamental coats always form a thick, but very soft capsule. In the course of early embryonic development, they lose water and progressively shrink until they form a rather thin compound ("multilayered") membrane (Fig. 2). Especially in *Sepia* eggs, this shrinkage is easily recognizable when one compares newly laid and moderately advanced eggs, the latter having a smaller size and a firmer consistency. In *Sepiola* and *Sepietta* eggs attached to one another, the shrinkage becomes clearly visible in the elongating junctions uniting eggs that stick together with their outer coats (Figs. 6). With the uptake of water by the chorionic contents, which are hypertonic against sea water (Russell-Hunter and Avolizi, 1967, De Leersnyder and Lemaire, 1972), the outer egg diameter then increases progressively so that the nidamental envelopes are stretched and grow ever thinner (Mangold-Wirz, 1963).

In *Rossia* eggs, the rapid hardening of the outer coat blocks the envelopes from stretching beyond the original diameter. The increase of the chorionic space related to the shrinkage of the soft envelopes thus ends when the inner egg shell diameter (minus the thin condensed nidamental layers) is attained. Although the outer coat of the eggs of Sepiolinae is elastic and allows some expansion at late embryonic stages, the size increase is rather limited. This is important for hatching, because the young animal has to prop its arms against the chorionic wall opposite to the hatch opening, as shown by Arnold *et al.*, (1972) in *Euprymna*.

ORDER TEUTHOIDEA

Most observations on spawning reported in the literature deal with myopsid squids of the family Loliginidae (Roper, 1965). The few available data on oegopsid squid egg masses nevertheless permit some generalizations. It seems reasonable to suppose that a nidamental apparatus comprising both nidamental and accessory nidamental glands represents the primitive condition of decapods. Such a common ancestral condition easily accommodates the supposedly derived teuthoid mode of serial egg encapsulation (maintaining the spiral enveloping mechanism). Instead of wrapping a single egg in a sheet of mucinous secretion, a string of eggs united by oviducal jelly is rolled into a common sheet of nidamental jelly (Figs. 7-9). The precise "cork screw" or "spiral stair" arrangement achieved by this process suggests that the wrapping occurs very rapidly at the outlet of the nidamental glands, i.e. before the jelly bands take up additional water to swell to the final size observed in the capsule when it leaves the mantle cavity. Evidently the number of eggs that can be enclosed in a single capsule is limited by both the size of individual eggs and the size of the nidamental apparatus, which in turn depends on the body size of the spawning female.

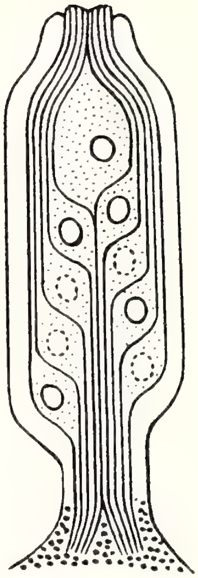


Fig. 9. A schematic presentation of a squid egg capsule (after Jecklin, 1934, modified). The coarse stippling corresponds to the fixating jelly, which grades into the (white) outer coat. The eggs are shown embedded in oviducal jelly marked by fine stippling. The lines represent the dense layers of nidamental jelly.

Not all squid egg masses are made of spirally coiled jelly layers, however. Ommastrephid squids produce extremely watery jelly masses that show no internal structure (Hamabe, 1961, Boletzky *et al.*, 1973, O'Dor, 1983). In some enoploteuthid squids, there are no nidamental glands at all, but the oviducal glands are extremely large (Naef, 1923).

ORDER VAMPYROMORPHA

Vampyroteuthis has no nidamental glands. The observed absence of jelly on pelagic eggs thought to be those of *Vampyroteuthis infernalis* Chun, 1903 (Pickford, 1949) is no proof that these eggs are released without any gelatinous material surrounding the chorion. It seems indeed more likely that the well developed oviducal glands produce a fragile jelly (providing some buoyancy?) that easily disintegrates when eggs are collected with nets.

ORDER OCTOPODA

The living octopods fall into two very distinct groups, the Cirrata (finned octopods) and the Incirrata.

SUBORDER CIRRATA

These deep sea animals encapsulate their very large eggs in a hard shell. The few eggs so far described (Boletzky, 1982a) show some variation in the structure of the egg shell, and also in its size relative to the chorion size. In only one case was the chorion surface separated by a wide, jelly-filled space from the outer shell (Fig. 10a). The surface of the shell, which is produced by the large oviducal gland (Aldred *et al.*, 1983), is smooth in some species, coarse (Fig. 10b) or distinctly sculptured in others. Such sculpturing sug-

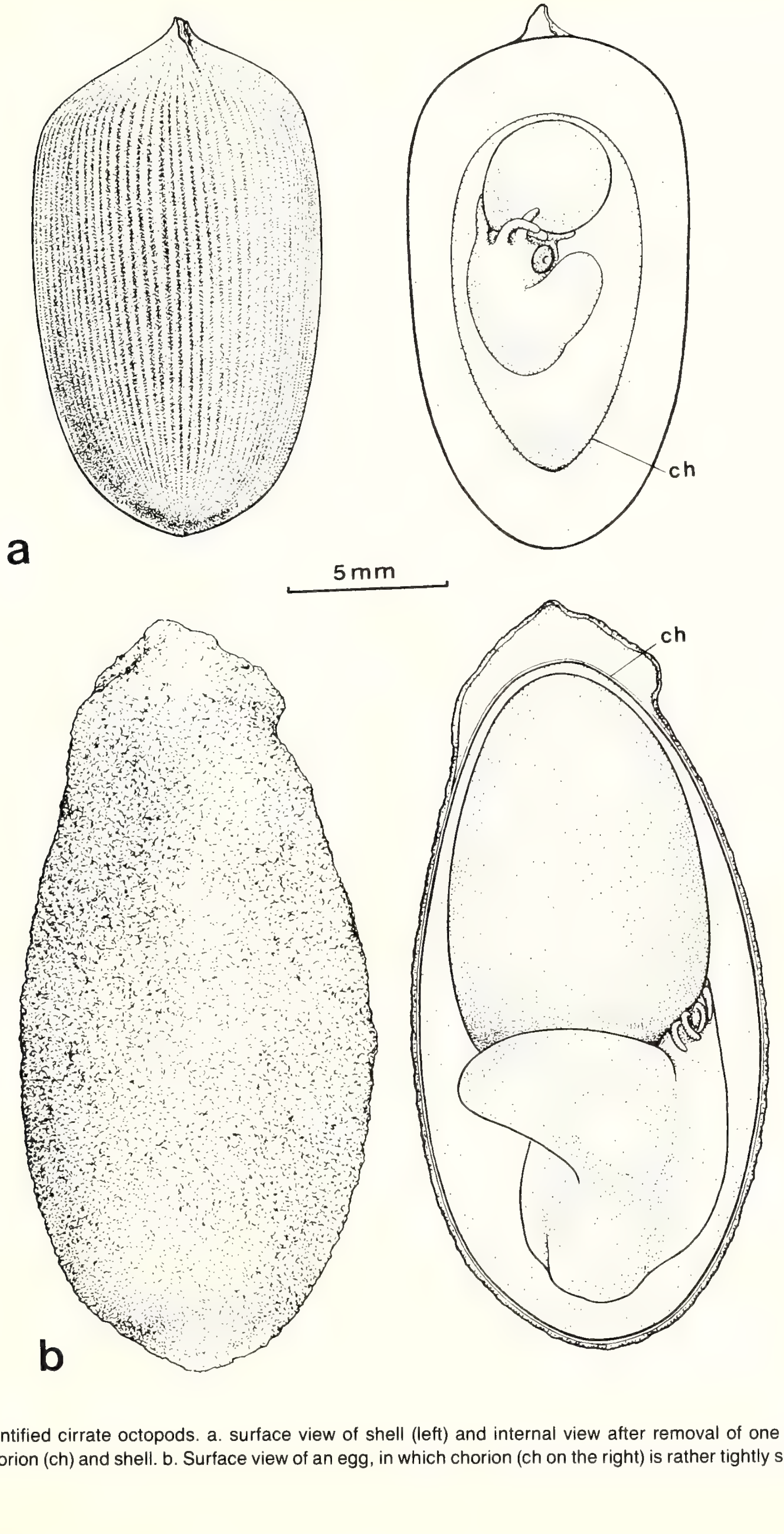
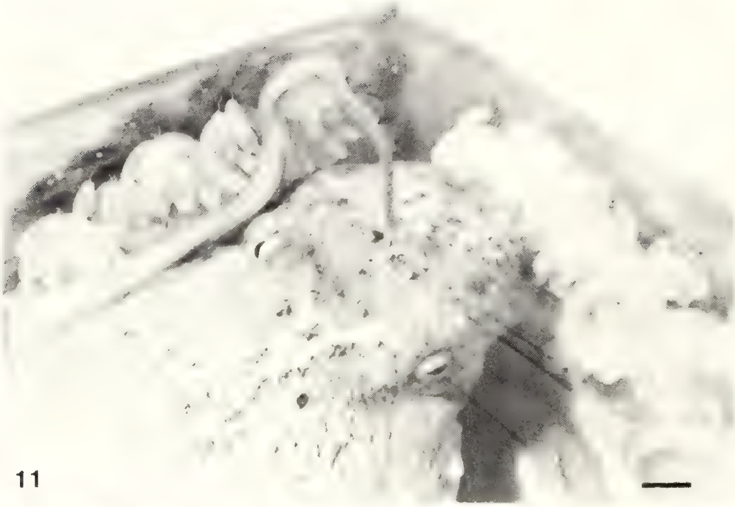


Fig. 10. Eggs of unidentified cirrate octopods. a. surface view of shell (left) and internal view after removal of one half of the shell. Note wide space between chorion (ch) and shell. b. Surface view of an egg, in which chorion (ch on the right) is rather tightly surrounded by the shell.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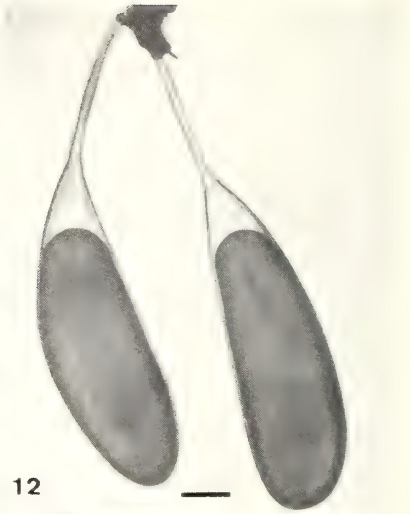
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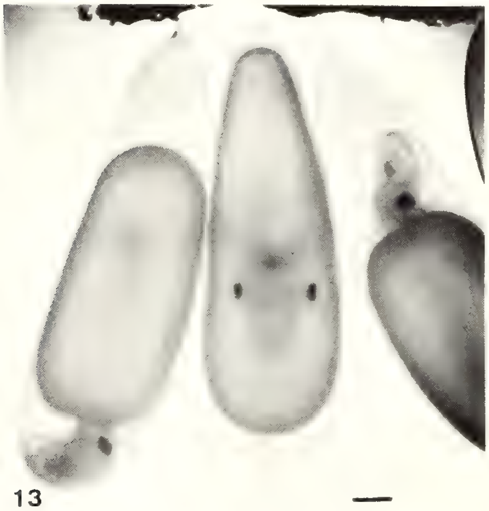
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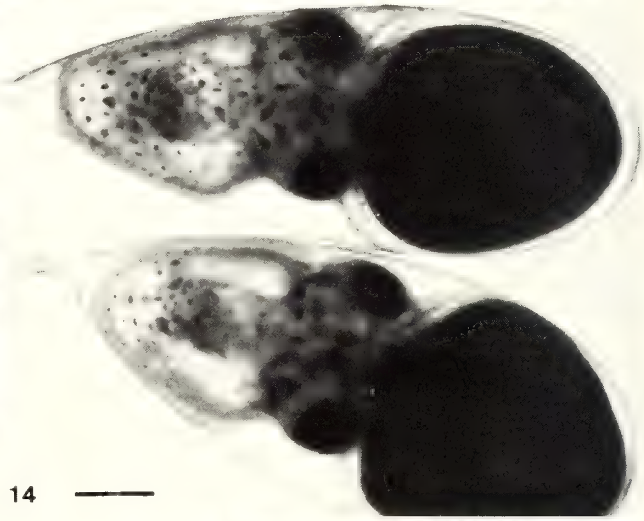
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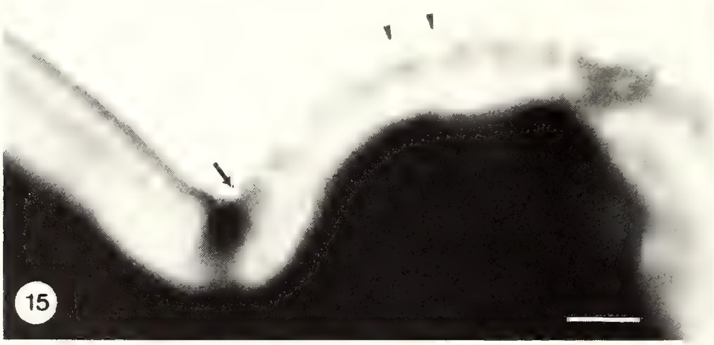
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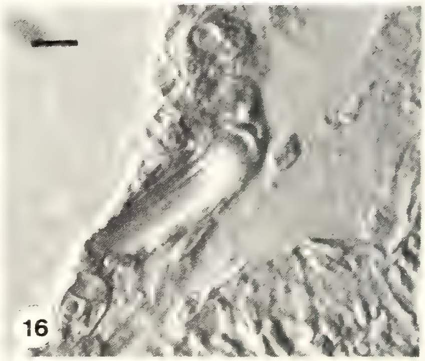
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Fig. 11. A female *Eledone moschata* brooding her eggs in the corner of an aquarium tank. Scale bar = 1 cm. **Fig. 12.** Newly laid eggs of *Pteroctopus tetracirrhus.* Note the rather short, thick chorion stalks fixed to a common base of oviducal "cement". Scale bar = 1 mm. **Fig. 13.** Eggs of *Octopus briareus* attached by the chorion stalk to a common axis (above). Note the different positions of the embryos due to delayed inversion (middle) or absence of inversion (left). Scale bar = 1 mm. **Fig. 14.** Advanced embryonic stages of *Eledone cirrhosa*, with a still large outer yolk sac (at right). Note that the embryo is very tightly surrounded by the chorion. Scale bar = 1 mm. **Fig. 15**. Detail view of an embryo of *Octopus vulgaris* (cf. Fig. 17) hatching from the chorion (at left). The arrow points to the edge of the hatching slit. Arrow heads indicate organs of Koelliker seen through the transparent skin. Scale bar = 0.1 mm. **Fig. 16**. Histological section of the skin of an *Octopus vulgaris* hatchling, showing an organ of Koelliker with its setal core anchored in the basal cell (above) and its outer end lying under a very thin tissue membrane (below). Scale bar = 10 μm.

gests that the shell hardens before the egg is released from the oviduct. Nothing is known of the laying procedure. In particular it is not clear whether the eggs are fixed to a specific substrate.

SUBORDER INCIRRATA

The members of this suborder invariably produce eggs devoid of protective capsules. The chorion is always drawn out into a stalk, the length of which is very variable among species (Figs. 11-13). The material secreted by the oviducal glands (Froesch and Marthy, 1975) normally surrounds only the end of this stalk and serves to fix it either directly to a substrate (Figs. 11, 12) or to other egg stalks thus forming the central axis of a festoon-like egg string (Fig. 13). Eggs are always actively protected by the female throughout the time of embryonic development (Fig. 11). In the Octopodidae, which are the only bottom living incirrates, females generally attach eggs or egg strings to a hard substrate, inside a shelter, and remain with them for the entire brooding time; this may last a full year in certain coldwater species producing very large eggs, as for example *Bathypolypus arcticus* (Prosch, 1849) (cf. O'Dor and Macalaster, 1983).

In a few octopus species, the females carry their egg strings or clusters in their arms (e.g. Tranter and Augustine, 1973). This method closely resembles the brooding habits of pelagic incirrates. Among these, *Argonauta* produces an elaborate auxiliary apparatus in the form of a calcitic brood shell, in which the eggs are carried. A simpler type of egg carrier is produced by *Tremoctopus* females. Instead of secreting organic material and calcium carbonate in the form of a thin-walled shell, the dorsal arms of the female produce short rods to which the eggs are attached (Naef, 1923). In both forms, the release of eggs is delayed beyond the first cleavage stages. This delay is pushed to true ovovivipary in *Ocythoe*,in which the eggs remain in the very long oviduct until the embryos are ready to hatch (Naef, 1923). The observations of Young (1972) on a bathypelagic octopus of the family Bolitaenidae suggest the existence of a special adaptation of the arm crown of the female to function as a brood pouch in this particular species (probably *Eledonella pygmaea* Verrill, 1848).

A feature common to all incirrates is the rather limited expansion of the chorion during embryonic development (Figs. 14, 17). Although the volume of the egg may increase by more than 150% during embryonic development, the embryo remains tightly surrounded by the chorion, which is much tougher than the decapodan chorion.

FERTILIZATION AND HATCHING

These two events mark the beginning and the end, respectively, of embryonic development. For both processes, egg capsules represent a barrier to be overcome as well as a substrate to be used for locomotory actions.

Except for octopods, in which fertilization is achieved in the oviduct or in the ovarian cavity (Mangold, 1983a, b), spermatozoa always have to cross some jelly material in order to arrive at the micropyle of the chorion. Depending on the site where spermatophores are stored after copulation (infrabuccal pouch, mantle cavity, etc.), and according to the capsular structure, access routes to the individual egg are shorter or longer for the spermatozoa. In all events, the consistency of the capsule material, which is still very soft at that stage, would seem to be important for penetration by the spermatozoa. The functional morphology of the latter should therefore be viewed on the background of locomotory requirements defined by the mucinous envelopes, across which they have to move. This concerns the leading structure formed by the acrosome; the position of the flagellum (or flagella) in relation to the posterior part of the sperm head; and the structure of the spine-like posterior process of squid spermatozoa (Fields, 1965, Franzen, 1967, Millard de Montrion, 1984), also called mitochondrial spur (Fields and Thompson, 1976).

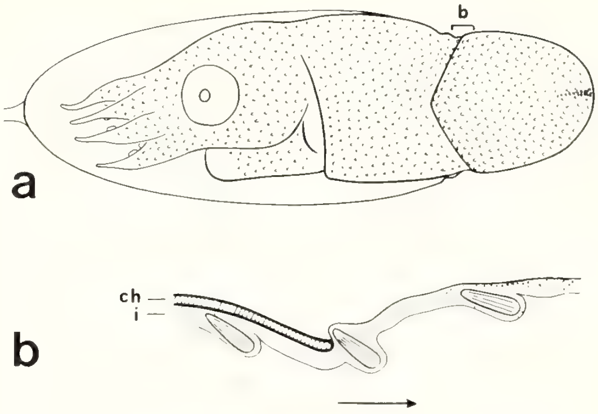

Fig. 17. A schematic presentation of hatching in *Octopus vulgaris* (or any other species of *Octopus* producing small-sized hatchlings with short arms). The arrow head points to the hatching gland (transversal bar of cells). The dense distribution of Koelliker organs is represented schematically in a. In b, a schematic longitudinal section of the skin at the hatching slit is given, corresponding to the area marked in a (see also Figs. 15, 16). The long arrow at the bottom indicates the direction of the hatching movement. ch = chorion, i = integument.

At the moment of hatching, similar constraints arise when the young animal has to move across the capsule material in a direction opposite to that of the spermatozoa. Meanwhile, however, the consistency of the capsule material has thoroughly changed. In all cephalopod hatchlings, the leading structure of the animal when moving across the capsule wall is the mantle end, which is equipped with a hatching gland (organ of Hoyle). This organ forms at late embryonic stages. It is made of special glandular cells of the epidermis which store proteolytic enzymes (cf. Denucé and Formisano, 1982). In the decapods, these cells are arranged in one dorsal and two lateral branches forming together an anchor-shaped complex. In the octopods, there is only one transversal band of glandular cells, which are less prominent than in the decapods (Fig. 17).

How hatching is triggered in cephalopods is still obscure. Probably all cephalopod embryos are kept "quiet" by a tranquillizing factor contained in the perivitellin fluid (Marthy *et al.*, 1976) so that premature hatching is largely prevented. How the threshold set by this system is finally overcome in the absence of artificial stimuli (which easily trigger hatching in the aquarium) remains to be demonstrated. The hatching process generally starts with characteristic stretching movements of the mantle, which seem to rupture the apex of the gland cells (Orelli, 1959). The enzymes thus released onto the chorion wall immediately dissolve it locally. Indeed in all known cephalopods, the position of the hatchling inside the chorion and the limited expansion of the latter have the effect of bringing the hatching gland into very close contact with the wall. Recent experiments (Boletzky, unpubl. results) have shown that the enzymes of the hatching gland are not species-specific. Loliginid hatchlings artificially enclosed in envelopes of a different species *(Loligo vulgaris* Lamarck, 1799, *Alloteuthis media* [Linnaeus, 1758]) were able to hatch out, and hatchlings of both the above-mentioned species were able to open the thick chorion of newly laid eggs of *Sepia officinalis* Linnaeus, 1758.

The role of the organ of Hoyle has been known since Wintrebert (1928) demonstrated its function as a hatching gland. Furthermore Jecklin (1934) has shown that there is no preparatory softening of the chorion, and that perforation of the chorion and the surrounding membranes is achieved solely by the instantaneous action of the hatching gland secretion. However, the importance of auxiliary processes in hatching have largely been ignored. Indeed hatching depends on both the *perforating action* of the organ of Hoyle and the *locomotion* generated by other organs of the hatchling. A close correlation between the capsule architecture and the lay-out of the entire hatching apparatus is clearly recognizable in the representatives of the Sepiidae, Sepiolidae, Loliginidae and Octopodidae so far studied (Boletzky, 1982b).

In *Sepia officinalis*, as in all decapod embryos, the skin contains very numerous ciliary cells. The motile cilia all beat in anterior direction (i.e. the effective stroke is directed away from the posterior mantle end). Together with the ciliature of the outer yolk sac (which disappears only towards the end of embryonic development), these cilia maintain the perivitellin fluid in continuous circulation. The three branches of the hatching gland are surrounded by ciliary bands that are distinct from the ciliary tufts covering the rest of the body. At the moment of hatching, the cilia of these bands are the first to be in contact with the edges of the hatch opening and they probably assist in providing a slight locomotory effect (cf. loliginid squids, below).

In contrast, in the Sepiolidae, there are no ciliary bands. The skin is only covered with rather widely scattered ciliary tufts. The rear end of the hatching gland is underlain by a peculiar conical organ, the so-called terminal spine (Naef, 1928). The tip of the spine is made of very dense connective tissue grading into a muscular basis anchored on the mantle musculature. Artificially immobilized hatchlings exposed to certain tactile stimuli go through rapid stretching movements during which the terminal spine strongly projects over the mantle end, thus demonstrating the autonomous contraction of the muscular basis of the terminal spine (Boletzky, unpubl. obs.). The punctual pressure achieved by this autonomous contraction is no doubt important in breaking the hard outer shell of *Rossia* eggs. This action is possible only in limited space allowing the animal to prop its arms against the chorionic wall when pushing the mantle end through the hatch opening.

In loliginid squids, the hatching apparatus is more similar to the situation observed in *Sepia*. However, instead of being limited to the immediate vicinity of the hatching gland, the distinct ciliary bands cover a large part of the upper and lower mantle surface. Live observations have shown that the relatively short cilia of these bands have only a very limited effect in circulating the perivitellin fluid, in contrast to the long cilia of the tuft cells (Arnold and Williams-Arnold, 1980). These short cilia appear to provide most of the locomotory effect obtained on the gelatinous substrate made available to them by the action of the hatching gland. The latter indeed acts like a "bore head" opening a tunnel in the nidamental jelly layers. Regardless of the initial direction a squid hatchling takes within the common egg capsule, it automatically arrives at the capsule surface by purely ciliary locomotion (Boletzky, 1979). Observations on *Illex* hatchlings indicate that the same mechanism allows these extremely small animals to leave the large jelly mass typical of ommastrephid squids (O'Dor, 1983).

A completely different arrangement characterizes the incirrate octopods. The skin of the hatchling is devoid of motile cilia. The transversal band of cells forming the hatching gland (Orelli, 1959) produces a slit in the chorion (Fig. 17). Only the mantle end is extruded due to the release of pressure from the elastically stretched chorion. Its contraction is insufficient, as in decapods, to expulse the animal. Although the octopus hatchling has to free itself of only one simple membrane, it is momentarily stuck with the greater part of its body still inside the envelope. Two structures are important in overcoming this situation: 1. the simple slit produced in the vaulted end of the elongate, relatively tough chorion presents a relatively sharp edge (Figs. 15, 17), and 2. the skin of octopus hatchlings contains a dense set of hard rod-like structures (the setal core of the organs of Koelliker), which together form a shingle-like surface preventing the body end from slipping back into the chorion (Figs. 16, 17). Indeed the setal core of each organ of Koelliker lies in an oblique position, its outer end pointing anteriorly. Although it is covered by a thin tissue membrane (Fig. 16), it slightly projects under the external pressure exerted by the sharp edge of the hatching slit (Fig. 15), allowing gliding of the skin in only one direction: outward. Thus, one-way movement is generated by repeated, rapid stretching of the body (Boletzky, 1978-79).

Within the benthic family Octopodidae, many species produce large eggs from which large hatchlings develop that already have long arms with many suckers. These animals use their arms to crawl out through the hatch opening. In contrast, in most small-sized hatchlings with short arms, the arms are not used during hatching (but see Boletzky, 1984, for an exception to this rule).

ECOLOGICAL ASPECTS OF ENCAPSULATION

Cephalopods are found in virtually all marine environments, in inshore waters as well as in the open ocean from tropical to circumpolar latitudes, in surface waters and at great depths. At virtually all depths, cephalopods having different life styles coexist in the near-bottom water layer, so that eggs laid on the bottom may be those of nektonic or of demersal and benthic cephalopods. In contrast, in midwater only eggs of midwater species are found.

Hard egg shells appear to be typical of benthic and bentho-pelagic cephalopods laying large eggs at great water depths or at high latitudes (*Nautilus, Rossia*, cirrate octopods); together the size of the eggs and the low water temperatures result in long embryonic development. However, alternative solutions to the problem of long term protection of the embryos do exist. Thus *Sepia orbignyana* Férussac 1826, a species living in rather deep water, inserts eggs into the oscula of sponges (Naef, 1923). The elongate shape and the transparency of the egg case are reminiscent of large incirrate eggs, but in contrast to the statement of Naef (1923) saying that "complete jelly coats are not produced", it must be stressed that the chorion of these eggs is surrounded by the typical spirally coiled nidamental jelly and a rather tough outer membrane, all of which are unstained. Thus the sponges do not replace the protective function of capsules; they provide *complementary* protection against predators (camouflage), and they also maintain a steady water exchange around the egg capsule. Females of *Sepia elegans* Orbigny, 1835, generally fix their eggs on branches of octocorallians (Bouligand, 1961) so polyps completely surround the egg. Finally the incirrate habit of brooding the eggs has also proved successful at great water depths. However, under these conditions, apparently only the "holobenthic" mode is represented by octopodids producing large eggs, whereas in shallower waters, this mode coexists with the "merobenthic" alternative that is characterized by a planktonic juvenile phase as shown by sympatric occurrence of octopodid sibling species distinguished by these adaptive strategies.

The *holopelagic* life cycle of the nektonic incirrate octopods, which produce large numbers of offspring of small individual size, is in many ways similar to that of squids producing floating eggs and egg masses, but in contrast to these, the nektonic incirrates invariably provide active protection in the form of "brooding" or ovovivipary.

Loliginid squids always fix their egg capsules to a substrate, either in such a way that the capsules hang from the point of fixation, or that they stick to sand particles or coarser substrata. The latter mode seems to be correlated with the production of very watery capsules having minimal weight in sea water, so that they move freely around the point of fixation and are thus continually flushed by water movement (Roper, 1965).

High water content of egg capsules clearly provides some protection against desiccation, as demonstrated by viable eggs collected on beaches above the water line, or from trawl nets that had been out of water for hours. Especially the eggs of *Sepia officinalis* are often washed ashore with the algae or grass weeds on which they are frequently laid. Under natural conditions, the embryos thus removed from their normal environment have a chance to survive only if they have not been exposed to high temperatures, and if they are again immersed, for example by a high tide. The apparently "wasteful" habit of many cuttlefishes and neritic squids of fixing their egg masses to easily detachable substrates must be counterbalanced by relatively high fecundity, i.e. high energy investment in both gamete and capsule production (Boletzky, 1981). In return, this behavior opens the possibility of "rafting" of eggs. Especially in *Sepia*, which remains close to the bottom and on the bottom throughout its life time, this may provide a means of dispersion of offspring.

DISCUSSION

Ecological aspects of encapsulation inevitably raise questions on adaptation, which can only be considered from the viewpoint of evolution. No matter to which particular theory of evolution one subscribes, the processes involved in adaptation appear complex. The present paper presents an attempt to find correlated processes in the life cycle of different cephalopods that have something to do with encapsulation. If particular features of encapsulation are viewed as the result of evolutionary change, it is legitimate to wonder which changes in adult, juvenile or embryonic morphology and physiology may be related to the former. Clearly some speculation is involved here, but it is perfectly acceptable as long as it is only used to handle established facts (not hypotheses).

In surveying different cephalopod groups, the foregoing sections have provided a number of arguments allowing one to suggest correlated changes in capsule structure, functional morphology of spermatozoa and skin structures of hatchlings. Within the decapods, the modifications are relatively clear, although several details remain to be clarified. As an example, the obscure phylogenetic position of the Sepiolidae (do they really belong to the Sepioidea, with which they share the character "eggs laid singly"?) raises a few problems; one is the questionable homology of "outer case" material in the egg capsules. Apart from this uncertainty, the homology of capsules and capsule-producing glands within the decapods is not called in question, however.

What can be said in this respect about the octopods? They lack nidamental glands in the mantle cavity, as do the Vampyromorpha, which are no doubt closely related to the Octopoda (see e.g. Young, 1977). Does their reproductive apparatus represent an ancestral condition? Assuming that it does would mean that nidamental glands in *Nautilus* and in decapods are analogous (evolved convergently), not homologous structures. This seems less likely than their homology. Consequently the absence of nidamental glands in the Vampyromorpha and Octopoda appears derived from a decapodan condition. Does this mean that nidamental glands have simply been *lost*?

Here speculation definitely has to come in if the question is to be pursued any further. But speculation can be firmly "based" on an embryological fact: the oviducal glands of both the decapods and the octopods are formed by an ectodermal invagination (see Marthy, 1968). In decapods, the nidamental glands are formed later on by an adjacent ectodermic territory (Lemaire and Richard, 1970). In the early morphogenetic processes, synchronization of organogenesis in both these territories, and "lengthening" of the invagination would suffice to include the nidamental gland in the oviduct. My suggestion that such a process may have occurred at the outset of the vampyromorphan/octopodan line of descent is pure speculation. And yet, it may lead to a better understanding of the cirrate and incirrate modes of encapsulation, provided that the correlation between changes in organ development can be established.

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ABSTRACTS
BIOLOGY OF MOLLUSCAN EGG CAPSULES

VARIATION IN HATCHING SIZE IN THE PULMONATE SNAIL *HELISOMA TRIVOLVIS* (SAY, 1817). Brian R. Rivest, Department of Biological Sciences, State University of New York at Cortland.

Specimens of the pulmonate snail *Helisoma trivolvis* were collected from five sites in New York State and maintained in the laboratory. Egg masses laid by individual snails were reared separately until hatching. Although egg diameter did not vary among snails, an analysis of the hatchlings' shell lengths indicates that there were significant differences in the mean hatching sizes among the snails within each population, and that there were also significant differences in the mean hatching sizes among the different populations. It is inferred that the differences in mean hatching sizes were due to differences in the albumen allocated to the egg capsules.

FACTORS AFFECTING PATTERNS OF OVA ENCAPSULATION IN GASTROPODS OF THE GENUS *CONUS*. Frank E. Perron, Department of Biology, New England College, Henniker, New Hampshire.

The phenomenon of ova encapsulation has several implications for life history evolution in the genus *Conus*. Patterns of ova packaging vary both within and between species with respect to the allocation of reproductive energy among capsular material, ova and intracapsular fluid. At the interspecific level, species producing large, slowly developing ova enclose their eggs in stronger, more energetically expensive capsules than do species producing smaller, more quickly developing ova. In some species, capsules can account for up to 50% of total reproductive energy.

Superimposed on this interspecific pattern are intraspecific age- and size-specific changes in the allocation of energy among capsules, ova, and intracapsular fluid. In species of *Conus*, individual females grow considerably during their reproductive lives. Egg capsule size is related to female body size in *Conus*, and egg capsule volume increases at roughly the same rate as does annual ova production. However, since large capsules contain lower densities of ova than do small ones, growing females must increase the number, as well as the size, of the capsules they produce. As a result of this pattern of ova packaging, per ovum costs of encapsulation (parental care) increase with increasing female size and age. Since the number of eggs per capsule is linearly related to capsule surface area, declining densities of ova in large capsules can result from declining surface/volume ratios and a reduction in net gas transport per unit of capsule contents.

ABSTRACTS
CONTRIBUTED PAPERS

1986 A.M.U. MEETING
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MALACOLOGY IN THE SOVIET UNION. Clement L. Counts, III, College of Marine Studies, University of Delaware Lewes. Delaware.

As a result of a one month exchange visit to the Academy of Sciences of the USSR, arranged through the United States National Academy of Sciences, it was possible to meet with Soviet malacologists at three Soviet institutions. The Zoological Institute, Leningrad, continues to serve as the principal repository of molluscan systematic resources within the USSR. The major zoogeographic strength of the collections is the fauna of the Palearctic. The Zoological Institute, Baku, is involved in environmental toxicology studies of the Mollusca, principally in the areas of hydrocarbon pollution of fresh and brackish waters, as well as completing faunistic work for the *Red Book*, the Soviet list of rare and endangered species. The Institute of Zoology and Parasitology, Dushanbe, is engaged in faunistic, taxonomic, and ecological research on introduced species of molluscs.

A review of the 1977 survey of malacologists of the USSR (Amitrov, 1983) revealed 844 biologists, geologists, chemists, geographers, and veterinary physicians were engaged in malacological research. 566 of these were geologists, 271 biologists, and the remainder spread over the other disciplines. The majority of those malacologists responding to the survey had received their candidates degree. Of the subspecialties of malacology, the most frequently reported, in descending order of response, were systematics, general ecology, stratigraphy, morphology, general biology, and phylogenetics. Of the major bodies of water within and around the USSR, Soviet malacologists most frequently reported studying the Mollusca of the Caspian Sea, the Black Sea, the Pacific Ocean, and the Don River Basin. However, these researches were mostly paleontological. Most malacologists within the USSR conducted their studies (listed in descending order of frequency) within the Crimea, Ukrainian SSR, the Caucasus, Central Asia, and Siberia. A review of birth statistics for Soviet malacologists revealed that, as of 1977, most active scientists were aged 52 to 41 years (range = 86 - 19 years) and that normal replacement of retiring malacologists appears to be in progress.

PRAIRIE DU CHIEN, WISCONSIN REVISITED - 10 YEARS AFTER DREDGING, Marian E. Havlik, Malacological Consultants, La Crosse, Wisconsin.

In July 1976 about 100,000 cu m were dredged from the East Channel of the Mississippi River, Prairie du Chien, WI. Since then over 175 endangered *Lampsilis higginsi* have been recovered from the dredge disposal site. Over 1/2 of these specimens were likely alive at the time of the dredging. In the past 10 years this area of the Mississippi has seen increased pressures from many sources stressing 35 living naiad species. In 1978 about 50 barges a year were unloaded. In 1984 over 500 barges were handled at one facility; the number at the city harbor has remained around 25 each year. Scraped and broken living naiades have been observed in navigable areas 3 to 4 m deep and at the edge of the 60 to 120 m wide navigation channel suggesting that prop wash may deposit naiades some distance from their original position. Fleeting has occurred in several shallow areas causing demonstrable damage to the substrate, shoreline and living naiades; several dying gravid *L. higginsi* have been stranded at the water's edge apparently unable to reestablish themselves in the substratum after being impacted by barge fleeting.

After repeated trips to the area 1567 empty shells (821 whole and 746 discrete valves) have added to the understanding of this highly variable species but taxonomic problems cannot be solved without adequate numbers of preserved soft parts (to date 35 preserved). Of 72 additional living specimens seen briefly, 55 were permanently marked, and all were returned to the river. The species is consistently about 0.5% of any population.

Commercial clamming pressures have greatly increased over the past several years. This fact combined with a naiad die-off of unknown causes since 1982 further stresses the largest known population of *L. higginsi* as indicated in 1985 by larger numbers than usual of fresh-dead shells in several areas. Since 1981 consistently high summer water levels have caused considerable erosion of numerous islands.

A BIOTIC INDEX FOR NAIAD MOLLUSKS IN THE UPPER MISSISSIPPI RIVER SYSTEM. Marian E. Havlik, Malacological Consultants, La Crosse, Wisconsin.

I propose a biotic index for naiad mollusks to assess their ecological value in the Upper Mississippi River System (UMRS), particularly in sensitive areas recently identified by researchers and agencies. Weights (values) would be in groups from 1 to 10: the most common species would receive a value of 1 to 3, moderately common a value of 4 to 6, uncommon a value of 7 or 8, and most of the rare species would receive a value of 9 or 10. Not all rare species have a high value because sometimes their presence indicates a degraded habitat; other species are rare apparently because of the lack of host fish. Some species that appear to be rare in recent UMRS studies, such as *Anodonta suborbiculata* and *Lampsilis radiata luteola*, are given medium values because often these species occupy shallow water habitat not usually thoroughly searched (< than 20 m offshore). If a species is represented by pristine fresh-dead shell only, then the assigned value would be subtracted by one. Species represented only by weathered shell material are listed but not given numerical values. If extralimital or historic species, such as *Potamilus capax* or *Quadrula fragosa*, are ever discovered alive they would be given a value of 10. If juveniles 3 years of age or younger are found of a species with a value of 9 or 10, three extra points are given for each species thus represented. Juveniles of species in group 8 would be given one extra point. Based on recent records, *Magnonaias nervosa, Obovaria olivaria,* and *Quadrula metanevra* appear to be critical indicator species. If one or more of these species is not present at a site (defined as 0.5 mile length of river) then it is unlikely that any of the species with a value of 9 to 10 will be present. Examples of these indices have been applied to individual sites and various pools in the UMRS. Five numerical categories with values ranging from poor to excellent have been developed. The index could be easily revised to reflect future data on UMRS naiad species.

TWENTIETH CENTURY CHANGES IN THE FRESHWATER MUSSEL FAUNA OF THE CLINCH RIVER (TENNESSEE AND VIRGINIA). S. A. Ahlstedt, Tennessee Valley Authority, Norris.

This study investigated the current status of freshwater mussel populations in the Clinch River since first being reported by Ortmann (1918). Freshwater mussel species have declined from a reported 60 species to the 47 species identified in this study. Impoundments have drastically reduced the mussel fauna in the lower Clinch and mussels have failed to recolonize a portion of the upper Clinch below Carbo, Virginia, following two major toxic spills in 1967 and 1970.

SPERMATOGENESIS IN THREE SPECIES OF UNIONIDS (BIVALVIA: UNIONIDAE). M. Bowie Kotrla, Department of Biological Science, Florida State University, Tallahassee.

Light and electron microscopic studies of spermatogenesis in *Anodonta imbecilis, Elliptio icterina,* and *Villosa villosa* were performed to determine (1) whether differences in sperm morphology exist at the subfamilial level and (2) the relationship of phylogeny and fertilization biology to gamete morphology in internally fertilizing bivalves.

No interspecific differences were found in morphology or histochemical staining reactions of cells at any stage of spermatogenesis. Spermatogonia are grouped immediately adjacent to the acinar basal laminae, are attached to each other by septate desmosomes, and have nuclei in which the chromatin is organized into many small irregular clumps. Groups of spermatocytes are medial to the spermatogonia and are identified by the chromatin reorganization occurring prior to and during meiosis. During spermiogenesis, cytoplasmic volume is considerably reduced, nuclear elongation is accompanied by chromatin condensation, and mitochondria migrate toward the posterior end of the nucleus.

In addition to the typical spermatogenetic pathway outlined above, there is a second, atypical pathway involving spermatogenetic cysts. Early cysts consist of 2-32 densely packed masses of DNA each of which is surrounded by a small amount of cytoplasm. More mature cysts are loose aggregations of randomly oriented sperm. These results support the hypothesis of Coe and Turner (1938. *Journal of Morphology* 62:91-111) that the cysts differentiate into sperm morphologically identical to those produced in the usual fashion.

The head of a mature sperm has a bullet-shaped nucleus and very little cytoplasm. The midpiece consists of 5 spherical mitochondria surrounding a pair of centrioles. The cone-shaped flagellar anchoring apparatus occupies the posterior end of the midpiece. The flagellar axoneme is of the typical 9 + 2 arrangement and originates from the distal centriole.

The unusual morphology of these sperm indicates that unionid fertilization may not occur in the manner previously supposed and reconfirms the diversity of sperm types among bivalves.

A PRELIMINARY EXAMINATION OF GEOGRAPHIC VARIATION IN A SIMULTANEOUS HERMAPHRODITE, *ANODONTA IMBECILIS* (BIVALVIA: UNIONIDAE): ELECTROPHORETIC AND HISTOLOGICAL EVIDENCE. Walter R. Hoeh, Museum of Zoology, The University of Michigan, Ann Arbor and Eileen Cordoba and Richard J. Trdan, Department of Biology, Saginaw Valley State College, University Center, Michigan.

Individuals of *Anodonta imbecilis* were collected at the following seven localities during 1985: Cedar River (CR) and Lake Contos (LC), Gladwin Co., Michigan; Appalachicola River (AR) and Mosquito Creek impoundment (MC), Gadsden Co., Florida; Ocmulgee River (OR), Ben Hill-Coffee Co. line, Georgia; Loch Raven Reservoir (LR), Baltimore Co., Maryland; Pickering Creek (PC), Chester Co., Pennsylvania.

Electrophoretic examination of gill tissue homogenates was performed on starch gels. Nineteen loci were scored. Fourteen (73.7%) were monomorphic across all populations. PEP-1, AAT, PGM, AO, and EST-1 displayed polymorphism within and among some populations. Bivalves from CR, LC, OR, and LR were monomorphic for all loci. AR and MC individuals displayed an extreme heterozygote deficiency. PC individuals were monomorphic for a unique allele at the PEP-1 and AO loci.

Histological examination of the visceral mass was performed using paraffin cross sections (7μm, H&E) from animals fixed in 10% buffered formalin. A ratio of testicular to ovarian tissue area was determined for each individual. The ratios across populations and geographic regions were analyzed using non-parametric statistics. Michigan (CR + LC) vs. East Coast (LR + PC) and "Florida" (AR + MC + OR) vs. East Coast populations had significantly different ratio distributions. The three geographic regions, in order of decreasing testicular/ovarian ratios, are East Coast > "Florida" > Michigan. In addition, the gonad organization in PC individuals was unique. Eggs and spermatozoa were seen together in the gonoducts of some individuals from CR, AR, MC, and OR. One gamete type was never observed without the outer type being present.

In summary: 1) there is a geographic component to the variation seen in the testicular/ovarian ratios, 2) electrophoretic and histological evidence suggest an additional species (PC) may exist on the Northern Atlantic Slope, 3) electrophoretic and histological evidence are consistent with a hypothesis of self-fertilization in some populations.

TAXONOMIC AND BIOCHEMICAL CHARACTERIZATION OF FLORIDA ELYSIIDAE USING STARCH GEL ELECTROPHORESIS. T. R. Nutall, Florida Institute of Technology, Melbourne.

Electrophoretic methods were used in the taxonomic resolution of Ascoglossan species. The consistancy of enzyme banding patterns within a species was determined using four species (three congeneric and one confamiliar) of Elysiidae. These patterns were then compared between species and used to construct a dichotomous key. Banding frequencies were used to calculate genetic identities and distances from which a phylogenetic tree was constructed. Specimens of the four species (*Elysia tuca* Marcus, 1967; *E. subornata* Verrill, 1901; *E. papillosa* Verrill, 1901; *Tridachia crispata* Mörch, 1863) were collected from Florida's eastern and southern coasts, starved for 24-48 hours, and frozen at -70ºC. Each specimen was gently ground up and the homogenate electrophoresed on a horizontal starch gel. The gels were stained to detect the presence of one of five enzymes: glucose phosphate isomerase, phosphoglucomutase, aminopeptidase I, esterase, and malate dehydrogenase. All four species possessed some allozymes that were extremely (>95%) consistant, regardless of geographic and morphological differences among individuals. *Elysia tuca* and *E. papillosa* were electrophoretically indistinguishable except at rapidly evolving loci (coding for esterase and aminopeptidase I). Enzyme banding patterns are an inexpensive and objective taxonomic tool for distinguishing closely related species of the Elysiidae. Banding patterns can be used to construct a dichotomous key, and band frequencies can be used to generate evolutionary distances and phylogenetic relationships.

MORPHOLOGY OF THE GILL GLANDS IN EUDORIDOID NUDIBRANCHS. M. Jonas, Friday Harbor Laboratories, Washington.

The gill glands of *Archidoris pseudoargus* and *Peltodoris atromaculata* are located at the base of the gills. Size and number of the glands increase with the size of the gills. The glands lie in the collagenous connective tissue that separates the afferent and efferent gill vessels. Narrow arborescent ducts lead from the gill surface to the glands. Each gland consists of glandular cells and supporting cells that form a more or less spherical organ with a small eccentric lumen. The fine structure of the glandular cells shows a large nucleus at the cell base and numerous membrane-bound secretion granules containing an electron dense material scattered throughout the cytoplasm. A thin basal lamina separates the gland from the surrounding hemolymph space. The cell surface of the supporting cells bears many cilia that fill the lumen of the gland. No secretion granules are to be observed in the lumen. The function of the gill glands is not known. Histochemical tests for the presence of proteins and mucopolysaccharides in the gland cells were negative.

A COMPARISON OF THE MINUTE MARINE SHELLS OF MIDWAY ISLANDS WITH THOSE OF THE ISLAND OF HAWAII. Bertram C. Draper, Los Angeles Museum of Natural History, California.

After two years of research on the minute marine shells of Hawaii, I had the opportunity to study and identify similar shells collected by Donald R. Shasky in twelve locations at Midway Islands, representing over 160 species also found at Hawaii. Midway was formed about seven million years ago while Hawaii is about one million years old on its west side and only a few thousand years on the east side. The ocean currents flow from east to west on both sides of the 1500 mile chain of islands between Hawaii and Midway, thus migration by ocean currents is from the newest island to the oldest. All specimens from Midway are from depths of two to eight meters, while many of the 300 plus species from Hawaii are from greater depths.

Noticeable differences were mainly in color and/or sculpture, but were limited to only about 30 species of the 160 studied. The variations were found mostly in species that live by filter feeding or grazing. These species are less likely to be replenished by migration in the currents, so are more likely to be affected by evolutionary changes at the older Midway atoll. Differences in numbers of any species collected at the two areas were disregarded due to the limited period of collecting at Midway.

Species cited for differences in sculpture and color:
- *Euchelus gemmatus* (Gould, 1895)
- *Joculator ridicula* Watson, 1866
- *Leptothyra verruca* (Gould, 1845)

Species cited for differences in sculpture only:
- *Scissurella pseudoequatoria* Kay, 1979
- *Vanikoro cancellata* (Lamarck, 1822)

Species cited for differences in color only:
- *Gibbula marmorea* (Pease, 1867)
- *Tricolia variabilis* (Pease, 1861)
- *Schwartziella gracilis* (Pease, 1861)
- *Caecum septimentum* de Folin, 1867
- *Trivia exigua* Gray, 1930
- *Kermia aniani* Kay, 1979
- *Julia exquisita* Gould, 1862
- *Leptothrya rubricincta* (Mighels, 1845)
- *Rissoina ambigua* (Gould, 1849)
- *Lophocochlias minutissimus* (Pilsbry, 1921)
- *Cerithium placidum* Gould, 1861
- *Lienardia baltreata* (Pease, 1860)
- *Koloonella hawaiiensis* Kay, 1979
- *Kellia rosea* Dall, Bartsch & Rehder, 1938

Species cited for being found only at Midway in my study:

Alvania (*Alvania*) *isolata* (Laseron, 1956)
Euplica turturina (Lamarck, 1822)

Species cited for being found at Midway and Maui, but not Hawaii:

Barleeia sp.

Collecting done along the outer side of the atoll reefs at Midway would undoubtedly add many other species to the Midway total.

TOWARD A WORKABLE REVISION OF THE PHILINACEA (GASTROPODA: OPISTHOBRANCHIA: CEPHALASPIDEA). **P. S. Mikkelsen** and **P. M. Mikkelsen,** Harbor Branch Oceanographic Institution, Ft. Pierce, Florida.

Cephalaspidean superfamilies are separated by radular dentition, gross external form and shell morphology. A considerable degree of variability was noted, however, within the Philinacea, principally with reference to gross external morphology. Three groups are defined: long-footed shell-carriers (Philinidae, Scaphandridae s.s.), long-footed atypical forms (Aglajidae, Gastropteridae), and short-footed shell-draggers (Acteocinidae, with calcareous gizzard plates; Cylichnidae, with corneous gizzard plates).

The bullacean families Retusidae (lacking radulae) and Volvulidae (lacking radulae and gizzard plates) more closely resemble short-footed philinaceans than they resemble other bullaceans (Bullidae, Atyidae).

Preliminary cladistic analysis showed two stable groups: (1) long-footed philinaceans (Scaphandridae, Philinidae, Aglajidae, Gastropteridae) and (2) typical bullaceans (Bullidae, Atyidae). Short-footed philinaceans and the "bullacean" Retusidae and Volvulidae were inconsistent in grouping with other families, indicating that their affinities to either the Bullacea or the Philinacea are unclear. Additional anatomical studies and re-evaluation of their placement are warranted.

The use of taxonomic names based on fossil types for Recent species is justified based on established practice throughout malacology. Although some authors have suggested restricting the genus *Acteocina* to fossil forms because its internal anatomy is unknown, such action (if perpetuated) would hinder evolutionary analyses within the Cephalaspidea. Conchological features within *Acteocina* and other genera are sufficient for identification of species, allowing fossil and Recent forms to be equated.

SYSTEMATICS AND ZOOGEOGRAPHY OF THE MELONGENIDAE (GASTROPODA: PROSOBRANCHIA). **M. G. Harasewych**, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D. C.

Phenetic and cladistic analyses of anatomical and shell morphometric data are used to reconstruct the phylogeny of the family Melongenidae. DNA-DNA hybridization studies of selected taxa provide an independent data base for evaluating phylogenetic hypotheses and divergence dates as indicated by the fossil record.

MOLLUSKS FOUND ON RIO GRANDE BREAK-WATER. **E. C. Rios,** Museu Oceanografico da FURG, Fundacão Universidade de Rio Grande, Brasil.

The marine mollusks that live on Rio Grande Break-water were studied. The material was collected on supratidal rocks by the author and to a depth of 10 meters by scuba divers. A total of 20 species was recovered. The malaco-fauna is similar to that found on Rio Grande Break-water buoys (Rios, 1979) with the exception of *Littorina ziczac* and *Siphonaria lessoni*, never found on buoys.

RADULAR CONVERGENCE DUE TO DIET: AN OVERESTIMATED PHENOMENON? **Silvard P. Kool,** George Washington University, Washington, D.C.

Radulae from taxa representing about 20 thaidid genera were examined by SEM. Correlations between radular morphology, diet, and phylogenetic relationships were analyzed. Data suggest that: 1) radular morphology is largely independent of dietary habits; 2) radular characters may be conservative, rather than convergent; 3) radular characters could be more useful in reconstruction of thaidid phylogeny than has been assumed so far.

THE PALLIAL ADAPTATIONS OF *PERNA VIRIDIS* (BIVALVIA: MYTILACEA). **Brian Morton,** Department of Zoology, The University of Hong Kong.

In Hong Kong and throughout its large geographic range, the epibyssate mussel *Perna viridis* tolerates widely varying environmental regimes. Obvious physiological adaptations are matched by appropriate inter-population variations in life history traits.

This study of feeding structures and mechanisms in the mantle cavity exposes other, morphological, adaptations that facilitate occupation of waters varying widely in quality. Ctenidial collection areas are relatively small. Similarly, the sorting areas of the labial palps are small and the dorsal edges of the palps are extensively fused to either the visceral mass or mantle so that they rigidly project backwards into the mantle cavity and are thus intimately apposed to the ctenidia. The anterior sorting areas of the ctenidia and of the palps are mostly rejectory. Although of the basic mytilid pattern, and therefore resulting from the adoption of the heteromyarian form, the arrangement of the pallial organs, and their ciliary currents, reveals how *Perna* is able to occupy waters with high sediment loadings. The efficiency of particle rejection suggests that high turbidities do not limit *P. viridis* and that this can help account for the dominance this species displays in many hydrographic environments.

MICROSTRUCTURE AND SURFACE SCULPTURE IN EARLY SHELLS OF *BRACHIDONTES EXUSTUS* AND *GEUKENSIA DEMISSA*. **S. Cynthia Fuller.** Rutgers University, New Brunswick, New Jersey.

Ontogenetic changes in the shell structure were examined in the mytilids *Brachidontes exustus* and *Geukensia demissa*. Prodissoconch, interdissoconch and dissoconch specimens of laboratory-reared mussels were examined by scanning electron microscopy to determine patterns in surface sculpture and microstructure. X-ray diffraction and staining with Feigl's solution were used to detect changes in mineralogy.

Valves of *Geukensia demissa* lack a distinct delineation in surface sculpture to mark settlement, but a transition from commarginal to cancellate sculpture occurs at a postsettlement stage (at an average length of 709μm). X-ray diffraction analyses indicate that the aragonitic mineralogy of the larval shell is retained until after this transition in surface sculpture, when the shell becomes bimineralic. At approximately the same stage, a change from a homogeneous shell to a multi-layered shell with an outer calcitic layer takes place.

At an average length fo 623 μm, a transition occurs in the surface sculpture of *Brachidontes exustus*. This transition is correlated with a change in the microstructure from a homogeneous shell to a multi-layered shell. However, the outer layer remains aragonitic unlike the outer layer of the dissoconch in *Geukensia demissa*.

INVESTIGATIONS IN THE MICROSTRUCTURE OF THE PALLIAL EYE OF *CERITHIDEA SCALARIFORMIS* (PROSO BRANCHIA). **Thomas N. Rogge**, University of Southern Mississippi, Hattiesburg.

Cerithidea scalariformis (Say), a marine intertidal mesogastropod, has a pallial eye in addition to its cerebral eyes, that fits into the siphonal notch of the shell aperture. Using Eakin's phylogenetic theory of photoreceptor development (1963, 1968) it should be possible to predict the structure of the eye as either ciliary or rhabdomeric. According to Eakin, this mantle eye should be ciliary in nature. In histological sections, several aspects of the pallial eye are evident. The lens is composed of elongated cells with dark staining proximal nuclei. It is separated from a supporting acellular vitreous body by a basement membrane. This vitreous body also separates the lens from the retinal layer. The retina varies from one to several layers in thickness, the latter being in the area receiving the most direct light. A pigment layer surrounding the retinal layer also surrounds individual retinal cells. Microstructurally, the lens surface is coated with mucus covered microvilli. The distal region contains many secretory cells. The nuclei and other organelles are found distally. The acellular vitreous body is filled with free-floating mitochondria, lysosomes, vesicles, and loose aggregates of membranes. The photoreceptor cells of the retina have concentric membranes that originate from basal bodies of cilia. The membranes are formed by as many as fifteen separate cilia per membrane. There was evidence of rapid breakdown and reformation of the photic membranes, common in active photoreceptors. The surrounding pigment consists of many small granules with dense walls. This eye may have an important anti-predator function.

TEMPORAL AND SEASONAL VARIATION IN SHELL MICROSTRUCTURE OF *CORBICULA FLUMINEA* AND *POLYMESODA CAROLINIANA* (CORBICULIDAE: SPHAERIACEA) FROM MISSISSIPPI, U.S.A. **Antonieto Tan Tiu,** University of Southern Mississippi, Hattiesburg.

Bivalves' capability to produce different shell microstructural types as a response to changing environment is a compromise between the "desirable" state and the limitation of the genotype. Understanding the constraints and range of these parameters in their shells, is basic to the understanding of paleo and recent events that brought about these changes, biomineralization and molluscan phylogeny.

The internal shell surface microstructure of wild and caged (marked) *Corbicula fluminea* and *Polymesoda caroliniana* were examined seasonally from June 1985 to March 1986 (June 86 samples have yet to be examined). Other parameters examined seasonally were biomass and related parameters, and reproductive stages. Physico-chemical parameters of the water and sediment organic content were measured monthly.

Internal shell surface microstructure in both species reflects seasonal as well as habitat differences. Preliminary analyses suggest that certain shell microstructural types (i.e. spiral, pseudospiral, rosette, reticulate, etc.) are associated with high growth rate, condition index, langelier saturation index and cool temperature, but not reproductive stage or shell organic content.

A PRELIMINARY REVIEW OF *MYSELLA* (BIVALVIA, MONTACUTIDAE) FROM THE NORTHEASTERN PACIFIC. **Paul H. Scott,** Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, California.

Members of the genus *Mysella* are small bivalves that can be free-living or associated with infaunal and epifaunal invertebrate hosts. Eleven species are reported from the northeastern Pacific, although a thorough systematic treatment of the genus has not been published in this century. *Mysella tumida* (Carpenter, 1864) is the most abundant species with densities exceeding 100/m^2 in many habitats from Alaska to southern California. *M. tumida* exhibits tremendous variation in shell shape, which is possibly correlated with variation in sediment grain size and intensity of wave action.

Four new species of *Mysella* have been recently recognized in southern California. Three of the new species appear to be free-living, and one species is associated with hermit crabs.

MORPHOLOGICAL CONSEQUENCES OF SPATIAL AND TEMPORAL VARIATION IN AN INTERTIDAL BLACK ABALONE POPULATION. **B. N. Tissot,** Department of Zoology, Oregon State University, Corvallis.

A study was conducted on an intertidal population of black abalone, *Haliotis cracherodii*, at Laguna Beach, California to measure patterns of morphological variation present within the population and their relationship to potential selective factors. From July 1983 to May 1985, 707 individuals were tagged and measured for six shell characters.

There was pronounced spatial and temporal variation in abalone abundance, distribution in the intertidal zone, and relationships between morphological characters and vertical elevation. Temporal variation in types of damage on recovered shells suggests that variation in predation by *Octopus* was greater during the summer and early fall when stress due to desiccation was maximal and abalone were distributed higher in the intertidal zone.

Variation among individuals in the number and size of respiratory pores promoted spatial variation in intertidal distribution. As a result, morphologically dissimilar individuals were exposed to different selective regimes. Covariation among components of morphological variation and potential selective forces suggest that morphological variation within populations is established through the interactions of selection and variation in growth, and persists for several years.

FUNCTIONAL ANATOMY AND SYSTEMATICS OF *LITIOPA* AND *ALABA* (PROSOBRANCHIA: CERITHIACEA).

Richard S. Houbrick, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Alaba has been referred to the Planaxidae, Litiopidae, Diastomidae, Cerithiidae, and to a number of subfamilies in the latter family. *Litiopa*, while usually assigned to the family Litiopidae, has been thought to be related the Planaxidae, Rissoidae, or Cerithiidae. The genus *Diala*, is frequently considered a close relative to both *Alaba* and *Litiopa*. This unstable classification is due to lack of anatomical knowledge and taxonomic opinons based on vague, equivocal, conchological characters.

No comprehensive anatomical study of *Litiopa* or *Alaba* exists except for a paper by Kosuge (1964) on the anatomy of *Alaba goniochila*, which is incorrectly cited by him as *Diala goniochila* throughout, and often overlooked for this reason. This has led others to wrongly include *Diala* with the Litiopidae.

Alaba and *Litiopa* are highly adapted for algal habitats, the latter genus found exclusively on pelagic *Sargassum.* Members of both taxa have metapodial mucus glands that produce long, anchoring, mucous threads, thereby preventing dislodgement from the algae. They also share similar taenioglossate radulae and have nearly identical, many-whorled, ribbed protoconchs. Their egg masses and planktonic larval stages are also alike. The anatomical groundplan of *Alaba* and *Litiopa* is cerithiacean (open gonoducts, aphallate males), but both genera stand well apart from *Diala* and other members of the superfamily in having epipodial tentacles and a subcentral metapodial mucus gland. All of these morphological features suggest a close relationship between the two taxa, which should be regarded as members of the family Litiopidae.

SHELL ONTOGENY OF THE ANTARCTIC BIVALVE *LISSARCA NOTORCADENSIS*.

R. S. Prezant, University of Southern Mississippi, Hattiesburg.

Lissarca notorcadensis Melvill and Standen is a small, nonornamented bivalve with a wide circumantarctic distribution. This mollusc is commonly found attached by stout byssi to echinoid spines where it grows to a maximum size of about 7 mm long. During shell ontogeny there are significant changes in overall shape and microstructure. From the larval D-stage, the clam undergoes significant mytilization, adapting to apparent dense population clusters. Additionally, there is a progressive modification in hinge dentition including loss of juvenile denticles and growth of adult lateral teeth. Numerous pores that permeate the valves can be related to bioenergetic savings during biomineralization or a "catch zone" for termination of shell fractures. *L. notorcadensis*, like many other polar bivalves, broods its young and releases juveniles just post-D stage. There is a distinct shift from prodissoconch to dissoconch, a characteristic more typical of lecithotrophic forms that could reflect some ancestral trait. shell ontogeny and limited life history aspects discerned from this study reflect the development of maximum competitive abilities in this Antarctic mollusc.

PLANKTOTROPHY BY POTENTIALLY LECITHOTROPHIC LARVAE.

S. C. Kempf, Auburn University, Alabama and **C. D. Todd**, University of St. Andrews, Gatty Marine Lab, Scotland.

By general definition, planktotrophic larvae require an obligate planktic feeding period, while lecithotrophic larvae are considered non-feeding. Recent investigations suggest that some lecithotrophic larvae can benefit from feeding (Kempf and Hadfield, 1985. *Biol. Bull.* 169: 119-130). Fed lecithotrophic larvae of *Adalaria proxima* lose tissue mass more slowly and retain more lipid, protein, and carbohydrate than starved larvae. Active digestive cells with large heterophagosomes and endocytosed algal cells are found in their left digestive diverticulum. Fed and starved larvae of *Tritonia hombergi* have the same tissue mass and lack active digestive cells. These results suggest that larvae of *A. proxima* can supplement maternally derived yolk reserves by planktotrophy. Since fed larvae of this species still lose tissue mass as compared to newly hatched larvae, ingested nutrients are not sufficient to entirely supplement metabolized yolk. By feeding, larvae of this species may be able to metamorphose after longer planktic periods than would be possible on yolk reserves alone. Larvae of *T. hombergi* cannot supplement yolk reserves by feeding and can be considered obligate lecithotrophs. When the results for these larvae and *P. sibogae* (Kempf and Hadfield, 1985) are compared to each other and to those for obligate planktotrophic veligers, what appears to be a graded transition from obligate planktotrophy to obligate lecithotrophy can be deduced. The loss of nutrient assimilation ability by *T. hombergi* is due to loss of function in digestive cell lysosomal systems. It would appear that larvae of *T. hombergi* could regain the ability to assimilate ingested nutrients by virtue of one or a few mutations affecting the lysosomal systems of digestive cells.

SUPPORT OF SYSTEMATIC MALACOLOGY BY THE NATIONAL SCIENCE FOUNDATION. Alan J. Kohn, National Science Foundation, Washington, D.C.

The Systematic Biology Program of the National Science Foundation supports basic research on taxonomy, spatial and temporal distribution, adaptations, and evolutionary relationships and histories of all groups of organisms. Research grants are made primarily for studies of comparative and evolutionary biology and for taxonomic monographs and revisions. Over the past five years, the Program has made an average of four new grants per year in systematic malacology. At the present time, 12 projects are being supported. Eight of these concern gastropods (four each on prosobranchs and pulmonates), three are on cephalopods, and one is on bivalves. Research approaches to systematic problems in these groups include evolutionary morphology, evolutionary impact of different modes of larval development, biogeography, genetic variation within and between species, monographic revisions, and distribution in the fossil record. The NSF uses several criteria in evaluating research proposals. Intrinsic merit, including the likelihood that the research will lead to new discoveries or fundamental advances in its field of science, is especially important. Other criteria include capability of the investigator, adequacy of institutional resources, relevance to areas extrinsic to its research field, and its effect on the structure of the national scientific enterprise. Other modes of NSF support available to researchers in systematic malacology include dissertation improvement grants and postdoctoral fellowships in the environmental sciences.

TAXONOMIC POSITION OF THE LATE CRETACEOUS GASTROPODS "*HINDSIA NODULOSA* (WHITEAVES, 1874)" AND "*FUSUS*" *KINGII* GABB, 1864. L. R. Saul. Invertebrate Paleontology, Natural History Museum of Los Angeles County, California.

"*Hindsia nodulosa* (Whiteaves, 1874)" is neither a *Hindsia* nor a buccinid although it may belong in the Buccinacea. Gastropods previously identified as *Hindsia nodulosa* (Whiteaves, 1874) constitute a new genus and can be divided into three biostratigraphically significant new species. "*Fusus*" *kingii* Gabb, 1864, is neither a *Fusus* nor a fusinid. Gastropods previously identified as *Fusus kingii* Gabb also constitute a new genus, and it can be divided into four biostratigraphically significant species, three of which are new. Early Senonian species of these new genera are closely related to *Perissitys* spp. of early Senonian age, but each lineage diverges from the others. The new genera also apparently had geographic distributions similar to that of *Perissitys* occurring in Senonian deposits of Japan as well as of the West Coast of North America.

Zinsmeister (1983) placed *Nekewis* Stewart, 1927, and *Heteroterma* Gabb, 1869, in the same family as *Cophocara* Stewart, 1927 = *Perissitys* Stewart, 1927, thus including species formerly assigned to the Turridae within the family characterized by *Perissitys*. A new species of *Nekewis* of early Maastrichtian age greatly resembles "*Hindsia nodulosa*" of mid Campanian age.

FAUNAL RELATIONSHIPS OF THE WESTERN ATLANTIC ARCHITECTONICIDAE. Rüdiger Bieler, Smithsonian Marine Station at Link Port, Fort Pierce, Florida, **Arthur S. Merrill** and **Kenneth J. Boss**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Based on a forthcoming worldwide revision of the Recent species in the family Architectonicidae, the Western Atlantic architectonicid fauna has been compared with other such faunas in the Eastern Pacific, Indo-West Pacific, Eastern Atlantic, Mediterranean and with the fossil record in the Caribbean Tertiary. It is demonstrated that there are only small differences between West Atlantic, East Atlantic and Mediterranean architectonicid faunas; most species are shown to have an amphi-Atlantic distribution. Only three major architectonicid faunas are here recognized worldwide: Atlantic (including Mediterranean), Indo-West and Central Pacific, and East Pacific. Architectonicids are a slowly evolving group (this can be explained by their long-range larval dispersal that allows a constant gene flow across ocean basins); their major radiation leading to Recent species took place before the oceans separated in the Middle Miocene and Pliocene. The differences between the three modern architectonicid faunas can be explained by the post-Pliocene extinction of different parts of the Neogene stock in the Eastern Pacific and in the Atlantic.

PHYSIOLOGICAL RESPONSES IN SPECIMENS OF *MELAMPUS BIDENTATUS* EXPOSED TO SUBLETHAL CONCENTRATIONS OF 2, 4 D. Jay Shiro Tashiro and **Jennifer Chabot**, Kenyon College, Gambier, Ohio.

Broadleaf phenoxy herbicides like 2, 4-D have a systemic action and can enter aquatic ecosystems in plant detritus. We have begun preliminary studies that examine the effects of 2, 4-D on specimens of the salt-marsh pulmonate, *Melampus bidentatus*. This species is a common detritivore in temperate North Atlantic salt marshes, with a distribution stretching from New Brunswick to Texas. *Melampus bidentatus* is a species with an iteroparous reproductive strategy and a pelagic veliger larva. Members of this species are simultaneous hermaphrodites. Reproductive cycles are closely coupled to spring tide inundation of the *Melampus* habitat in the upper reaches of the intertidal zone.

We have been studying a population of *Melampus* from the little Sippewissett Marsh (Falmouth, MA). During the past five years, we collected a large empirical base on the life history, ecology, and physiology of specimens from this population. Recently, we turned to studies of sublethal physiological responses in specimens of *Melampus* that had been exposed to *Weedar*, a commercial herbicide formulated as a dimethylamine salt of 2, 4-D. Our experimental design was age-specific in context. We measured respiration and feeding rates in individuals of the three age classes dominating the Little Sippewissett population. Experimental treatments included immersion regimes (mimicking tidal inundation of water containing herbicide) and feeding regimes (ingestion of an artificial ration containing sublethal amounts of 2, 4-D).

Our results provide a catalogue of sublethal effects, manifest as changes in respiration, feeding behavior, and mobility. Our data indicate there is a need to carefully evaluate the movement of herbicides into detrital pools, the residence times of such herbicides, and the potential for sublethal toxicity in detritivore populations.

EVOLUTIONARY RELATIONSHIP BETWEEN FOSSIL AND MODERN *MICRARIONTA* (PULMONATA: HELMINTHOGLYPTIDAE) ON SAN NICOLAS ISLAND, CALIFORNIA.

Timothy A. Pearce. Department of Paleontology, University of California, Berkeley.

Micrarionta opuntia Roth, 1975 and *M. sodalis* (Hemphill, 1901) are helminthoglyptid land snails having morphologically similar shells. The two species are found only on San Nicholas Island, one of five southern California Islands where the twelve species of *Micrarionta* are endemic. Stratigraphic evidence, combined with radiometric dating indicates that *M. sodalis* existed on the island before 120,000 years ago, and *M. opuntia* appeared on the island in the latest Pleistocene roughly 18,000 years ago. The two species coexisted on the island with a gradual change in dominance from *M. sodalis* to *M. opuntia*, then *M. sodalis* became extinct less than 3400 years ago, while *M. opuntia* persisted. Morphometric analyses show that the shell of *M. opuntia* is morphologically more similar to that of *M. sodalis* than to the shells of any other species of *Micrarionta*. The stratigraphic evidence and results of the morphometric analyses support the view that *M. opuntia* evolved on San Nicholas Island from *M. sodalis* rather than having been introduced from elsewhere. Relative constancy in shell characters through time of the two species, bimodal frequency distributions of the two species in a number of size and shape characters, and stratigraphic evidence that *M. opuntia* and *M. sodalis* coexisted on the same part of the island while maintaining their distinct morphologies, indicates cladogenic evolution and confirms the taxonomic validity of the two species. A climatic increase in aridity, or activities of Native Americans may have been factors influencing the extinction of *M. sodalis.*

THE ULTRASTRUCTURE OF THE HERMAPHRODITIC DUCT EPITHELIUM IN *ANGUISPIRA ALTERNATA*.

Richard L. Reeder and **Susan J. McKee**, Faculty of Biological Science, University of Tulsa, Oklahoma.

The hermaphroditic duct of *Anguispira alternata* is similar in its gross morphology to that of other terrestrial pulmonates, being a tortuously coiled duct from the ovotestis to the talon-fertilization chamber complex. The lower three quarters of duct serves as a seminal vesicle. Histologically the duct is thin-walled throughout its length and consists of a complex epithelium and a thin layer of muscle, the latter gradually becoming more prominent in the lower regions of the duct. The present study focused on the cells of the epithelium. At least three cell types, and possibly a fourth, can be observed in the epithelial layer lining the lumen of the duct. The first is a squamous-type cell lining the outer curvature of the coils of the duct. These cells have few organelles and large amorphous nuclei. The inner curvature of the duct is lined by two basically cuboidal cell types, one staining light and one dark with uranyl acetate, lead citrate and osmium tetroxide. The darker cells appear sandwiched between the more robust light cells and have slender lateral interdigitations with the light cells. Both cell types possess cilia and microvilli and have abundant apical mitochondria. The light cell possesses Golgi in its basal regions and sometimes large vesicles. The nuclei of both cells appear similar in structure, although more vesicular in the light cells. A prominent basal lamina underlies the epithelial layer everywhere. The morphology and distribution of the fourth cell type is still under study. It appears cuboidal with microvilli only.

INVOLVEMENT OF TESTOSTERONE ON THE FUNCTIONAL DIFFERENTIATION OF THE PENIAL COMPLEX IN *CRYPTOZONA BELANGERI* (DESHAYES) (MOLLUSCA: GASTROPODA).

S. Rajasekaran and **Vijayam Sriramulu**, Department of Zoology, Annamalai University, Annamalai Nagar, India.

In the terrestrial pulmonate gastropod *Cryptozona belangeria* (Deshayes) progesterone, estrogen and testosterone have been found by using low frequency (80 MHZ) H^1 FT NMR spectrometer. Spectrographic pictures have also shown that the male phase gonad has a higher level of testosterone while estrogen is low. On the other hand, a higher titre of estrogen along with 17B-hydroxy-testosterone was characteristic during female phase. Since hormones usually act by binding to macromolecular receptors at the cell membrane surface or within the cells where the binding is specific in respect to the functional status of the target organ, the penial complex, a male accessor reproductive organ in *C. belangeri*, has been studied to analyse the bound hormone during the different reproductive stages using H^1 FT NMR spectrometer.

An increased level of testosterone bound with the penial complex has been noticed during the male phase of the snail with a characteristic decrease in the level of binding of testosterone in the female phase. Following tentaclectomy a reduction in the binding of testosterone is noticed, possibly due to a low level of testosterone as evidenced by an increase in the level of the intermediary structure 17-B hydroxy testosterone providing additional source of estrogen. The low level in the production of testosterone by the gonad following tentaclectomy has led to a regression of the penial complex as the lack of adequate titre of testosterone has failed to induce any conformational changes in the receptor site to activate the target organ.

It is evident from the foregoing observations that the gonad in *C. belangeri* is the source of hormone production and the tentacular principle wields some influence on the production of male hormone to activate the penial complex establishing a gonad tentacle axis. Since extirpation of the tentacle does not induce production of testosterone, the penial complex has regressed which suggests the prevalence of the optic-tentacle-gonad and penial complex axis.

CHROMOSOME NUMBER IN THE PHILOMYCIDAE. H. L. Fairbanks, Penn State University, Monaca.

The Philomycidae is a family of slugs comprised of four genera, *Meghimatium* (Japan, China), *Philomycus Pallifera* and *Megapallifera* (North and Central America). Prior to this study, the only chromosomal investigation of the Philomycidae involved two species of *Meghimatium* from Japan. For this study, specimens of three U.S. philomycids were collected. The procedures outlined by Babrakzai and Miller were used to prepare the ovotestis and make the slides. Fisher Scientific Giemsa stain was used to stain the chromosomes. Mitotic and meiotic spreads were obtained for *Philomycus carolinianus, P. togatus* and *Megapallifera mutabilis. P. carolinianus* and *P. togatus* had 25 pairs of chromosomes, *M. mutabilis* had 27 pairs. All three species had many polyploid nuclei in the ovotestis.

Pilsbry noted that the Philomycidae were "... apparently an early branch from endodontid stock which also gave rise to the Arionidae." Haploid numbers in the Arionidae range from 25 to 29, similar to the philomycids (24 - 27). Extant Endodontidae have haploid numbers of 29 - 31, indicating, perhaps, greater conservation of the ancestral condition in the slugs.

SHELL MICROSTRUCTURE OF CRETACEOUS CRASSATELLIDAE (MOLLUSCA: BIVALVIA): IMPLICATIONS FOR SUB-FAMILIAL CLASSIFICATION? George L. Kennedy, Section of Invertebrate Paleontology, Los Angeles County Museum of Natural History, California.

Weathered specimens of most, but not all, crassatellid species in the subfamily Crassatellinae from the Upper Cretaceous of western North America reveal a subsurface pattern of radial riblets that is an intra-shell manifestation of the denticles that lie along the inner margin of the shell. The pattern also is present in *Crassatella ponderosa* (Gmelin, 1791), the type of the genus from the Eocene of France, and has been used by Chavan (1969) in his characterization of the family. The presence or absence of radial riblets allows a rapid means of segregating Cretaceous crassatellins into two groups. The relationship of the radial riblets to shell microstructure, and their significance in classification at the subfamily or lower levels, has been investigated with the aid of scanning electron microscopy (SEM).

The configuration of shell layers in the Crassatellidae is reported to be relatively simple, comprising an outer, crossed lamellar layer that is separated from the inner, homogeneous layer by a thin pallial myostracum (Taylor, Kennedy, and Hall, 1973). Preliminary SEM examination of several nominal crassatellid genera and species with subsurface radial riblets reveals that the crossed lamellar layer is divisible into two parts, the outermost of which is comprised of distinctly larger first order lamellae than the inner part. In transverse sections, the boundary between the two parts appears as a rippled or wavy line that separates the outermost surface shell and marginal denticles from the infillings between denticles and the inner, extra-pallial part of the shell. However, Late Cretaceous crassatellids here assigned to *Pachythaerus*, such as *Crassatella vadosa* Morton, 1834, from the southeastern United States, and two new species from southern California and northern Baja California, exhibit a different arrangement. These species possess a denticulated inner shell margin, but lack any sign of subsurface radial riblets. SEM examination reveals a well defined outer, crossed lamellar layer, and a middle layer that probably can be assigned to the intersected crossed acicular structure type of Carter and Clark (1985). The boundary between the two shell types parallels the growth margin and shows no rippling effect.

Preliminary results of this study indicate that 1) shell microstructure should be taken into consideration in any systematic revision of the family, and 2) that North American and European Cretaceous and Tertiary species can be allocated into several suprageneric groups that are defined, in part, by details of their shell microstructure. Formalization of these divisions, perhaps at the tribe level, must await further study of fossil and Recent Crassatellidae on a world-wide basis.

APPLIED MALACOLOGY: NEW MOLLUSCAN DATA ON THE EVOLUTION OF THE GULF OF CALIFORNIA AND BAJA CALIFORNIA PENINSULA, MEXICO. Judith Terry Smith, 1527 Byron Street, Palo Alto, California

For years geologists considered the Gulf of California a Pliocene to Holocene (5.3 m.y. to present) embayment preceded by a "protogulf" that originated ca. 8 m.y. B.P. (before present). The area includes the boundary between the Pacific and North American Plates, a complex region of en echelon faults, spreading centers, and active volcanoes. Fossiliferous sediments associated with radiometrically dated volcanic rocks indicate that marine water was present in the area as early as 13 m.y. B.P., long before the Baja California peninsula began to separate from mainland Mexico (ca. 4 m.y. B.P.). Like the modern gulf, the ancient one had numerous abruptly changing facies containing mollusks of Tertiary Caribbean and Pacific Panamic affinities. It extended from the head of the Salton Trough to Cape San Lucas, as seen from Miocene mollusks in the Imperial Formation of California, Isla Tiburón, Arroyo San Nicolas, and near Santa Anita in the Cabo Trough. Marginal embayments of the early Gulf had more complex histories than previously thought; near Loreto, for example, extensive nonmarine sediments are interbedded with the shallow neritic facies that were deposited around islands of older rocks. In the late Oligocene to early middle Miocene, before there was a gulf, marine water on the Pacific side of Baja California had many of the same molluscan species as are found in the Gatun Formation of Panama.

New molluscan studies are focused on Gulf fossils to identify paleoecologic indicators, significant phylogenetic lineages, and the oldest occurrences of Tertiary Caribbean species. Geophysical models proposed for the tectonic reconstruction of southern California and west Mexico suggest that large sections of the continental borderland moved 300 - 2,500 km north in the last 20 - 100 m.y., large figures in need of refinement. So far, faunal data have not been incorporated in these models; when available, species distribution data will provide information on sources of terranes and constrain time intervals in which movement occurred.

ABSTRACTS LIFE HISTORY, SYSTEMATICS AND ZOOLOGY OF CEPHALOPODS SYMPOSIUM

Organized by Roger Hanlon
University of Texas
Marine Biochemical Institute

POPULATION CHARACTERISTICS OF OREGON *LOLIGO OPALESCENS*.

R. M. Starr. Oregon Department of Fish and Wildlife, Newport.

Length, weight, sex, and maturity data from over 5000 squid collected off Oregon from 1983-1986 indicate morphometric and physiological differences exist between Oregon and California *Loligo opalescens*. Mean dorsal mantle length of 3200 *L. opalescens* collected in 1985 was 130.1 ± 0.46 mm (95% CI), compared to the long term average length of 140-150 mm reported for squid from Monterey. Mean whole weights and mantle weights were correspondingly smaller than California *L. opalescens*. Mean mantle lengths were 111.2 mm and 110.8 mm in 1983 and 1984, respectively, probably reflecting the influence of El Niño conditions.

Population parameters exhibited differences in trends and patterns as well as differences in means. Females sampled had larger mean dorsal mantle lengths than males, and the mean mantle length of all samples decreased with time. *L. opalescens* spawned in aquaria produced the same amount of egg capsules per female as California squid, but only one-fourth to one-half as many eggs per capsule.

Weight to length relationships can be used to determine squid residence time on spawning grounds. The mean weight to length ratio of females decreases with an increase in the percentage of spawned females in the population. Thus, an increase in the mean weight to length ratio of a sample indicates that squid in an earlier spawning stage have moved into a spawning area. This technique is used to help evaluate the results of hydroacoustic abundance estimates of squid.

GEOGRAPHIC VARIATIONS ON REPRODUCTION AND SIZE STRUCTURE OF *ILLEX ILLECEBROSUS* WITH IMPLICATIONS ON ABUNDANCE AND RECRUITMENT.

M. L. Coelho, Dalhousie University, Halifax, Canada.

The population structure of the squid *Illex illecebrosus* is difficult to interpret due to a lack of information on age and reproductive patterns. After validation of maturity staging in relation to oogenesis and spermatogenesis, an analysis of data on length at maturity stage for a seventeen year period and for almost the entire geographical range was used to define three reproductive components of the species. The major component spawns in winter (A) with minor components in summer (B) and spring (C). Long and short term fluctuations of size at maturity stage in A seem to result from cyclic shifts of spawning. These changes are driven by the relative prevalence of A and B in the southern population which account for the variations of mean size at maturity and of maturity rates in the population. A model of the general population structure of *I. illecebrosus* is proposed that indicates changes in the reproductive potential of the whole population in the whole area. These changes in reproductive potential can produce the known drastic changes in abundance and recruitment. The changes of the biological characteristics are discussed in relation to environmental variations including those due to overfishing of some competitors.

LOCOMOTION OF *NAUTILUS*: ADAPTIVE DESIGN AND LIMITATIONS OF A SHELLED CEPHALOPOD,

J. A. Chamberlain, Jr. Department of Geology, Brooklyn College of CUNY, and Osborn Laboratories of Marine Sciences, New York Aquarium, New York Zoological Society, Brooklyn.

Like other cephalopods, *Nautilus* swims by jet propulsion. Yet, in most details of its locomotion, *Nautilus* differs markedly from softbodied cephalopods. In *Nautilus* locomotory thrust is developed by activation of the paired cephalic retractor muscles and muscles of the funnel. The cephalic retractor propulsive mechanism of *Nautilus* is weaker and more inefficient than the mantle muscle system of other cephalopods. This situation results from the small size of the locomotory muscles and mantle cavity in *Nautilus*. *Nautilus* propulsive shortcomings stem from retention of the shell as a hallmark of adaptive design. The large, heavy shell causes high drag, and precludes the possibility of packing body spaces with large volumes of muscle. The evolutionary history of cephalopods reflects the interweaving of the two great adaptive themes of buoyancy control and propulsion. Shelled cephalopods have declined partly because the shell has constrained evolutionary progress toward more effective propulsive systems. Fish and soft cephalopods have proliferated as a consequence of not being constrained in this way. Their buoyancy requirements are compatible with, and have helped foster, the efficient propulsive systems with which they dominate the modern seas.

AMMONIA EXCRETION IN THE CEPHALOPODS, *OCTOPUS VULGARIS, SEPIA OFFICINALIS* AND *LOLIGO FORBESI*.

R. Boucher-Rodoni, Station Biologique, Roscoff, **K. Mangold**, Laboratoire Arago, Banyuls-sur-mer, France.

Ammonia excretion was investigated in mature adults of three species of Cephalopods, the pelagic *Loligo forbesi*, the necto-benthonic *Sepia officinalis* and the benthic *Octopus vulgaris*. The accumulation of ammonia in the sea water reflected renal and extra-renal excretion. A continuous increase in the total concentration indicates that diffusion through the gill epithelium (and possibly other epithelia) is an important source of ambient ammonia.

The highest excretory rate was recorded in the squid *Loligo forbesi*. No striking sex related difference was observed between males and females of the same species, except for one hyper-mature squid female where ammonia excretion rate was increased. In *Sepia officinalis*, growth related differences were observed, the smaller individuals excreting relatively less ammonia than the larger.

The response of mature animals to experimental starvation depends on the nutritional condition and metabolic level of the animal at the beginning of food deprivation. During short periods of fasting, the rate of ammonia release is decreased. The animal using protein and lipid meatabolic substrate, before shifting to an exclusively proteinic metabolic source for energetic needs.

EXPERIMENTAL POTTING OF *OCTOPUS VULGARIS* OFF SOUTH CAROLINA, USA.

J. D. Whitaker and **L. B. DeLancey.** South Carolina Marine Resources Center, Charleston.

Octopus vulgaris was potted from August 1984 to June 1986 using several types of pots including 4- and 6- in. diameter PVC pipe sections (doubles - two pipes tied together), sections of automobile tires, and 4- and 6- in. septic tank drainfield pipes (single-pipe sections). Project personnel fished pots off Charleston, S. C. while contracted commercial fishermen potted off Georgetown, McClellanville, Little River and Charleston. Pots were fished in longline fashion, usually with about 15 pots per line in 12 and 21m of water. In Year I, 1984-1985, PVC and tire pots were tested and in Year II, 6- in. PVC (double) pots and drainfield pipe pots were used. Equal numbers of each type were placed alternately along the longline. Soak times were usually between five and fifteen days, but some soaks were much longer.

Through 12 May 1986, a total of 981 *O. vulgaris* was collected in 3,779 pots for an overall catch rate of 26.0 percent. The highest catch rates were observed in fall 1984 followed by summer 1985 and fall 1985. Fall 1984 catch rates averaged about 57 percent for all gears. Catch rates were similar for the various gears in Year I but the 6-in. PVC pots had the best catch rates in Year II. Catch rates dropped sharply in winter of both years and remained relatively low until summer. It appeared that lower winter temperatures resulted in an offshore movement. Limited observations from deeper water indicated that octopii were more abundant there during winter.

Good catch rates were observed after soaks of only two days but, generally, catch rates were best after five to seven days and did not improve substantially with longer soaks. Commercial fishermen were impressed with catch rates but most did not believe they could fish octopus profitably under current economic conditions.

The incidence of females with well-developed gonads and brooding females was greatest during spring. As catch rates in fall 1984 increased, average size increased from about 0.7 kg in October to about 1.6 kg (males) and 1.2 kg (females) in December. Average size was smaller in fall 1985. Data on length-weight relationships, morphometrics, prey items and other biological aspects were recorded.

AGE DETERMINATIONS OF THE LARVAE OF THE OMMASTREPHID SQUID *ILLEX ILLECEBROSUS* USING STATOLITH INCREMENT COUNTS.

Norval Balch[1], **Geoffrey V. Hurley**[2], and **Andre Sirois**[3]; The Aquatron Laboratory, Dalhousie University, Halifax, Nova Scotia[1]; Hurley Fisheries Consulting, East Postal Stn., Dartmouth, Nova Scotia[2]; Department of Biology, Dalhousie University, Halifax, Nova Scotia[3].

Statoliths of *Illex Illecebrosus* larvae from field samples and laboratory rearing experiments were examined for growth increments. After removal from the statocysts, statoliths were immersed in a drop of distilled water and examined using transmitted light microscopy. Growth increments were counted with relative ease on the resulting micrographs. After 7.5 day incubation of an egg mass in the Aquatron Laboratory, immediate post-hatch larvae showed no increments. Field samples with mantle lengths (ML) 1.8 - 2.9 mm had from 10 to 22 increments. Since earlier workers have established that increments are laid down on a daily basis, both by captive adult *Illex* (Dawe *et al*., 1985. *J. Northw. Atl. Fish. Sci.* 6:107-116) and laboratory-reared hatchling *Loligo* (Yang *et al*. 1986. *Fish. Bull.* In Press), we assume the field-caught *Illex* larvae were 10 to 22 days old. Since they were collected in mid-January, the spawning date for larvae of this size range would have been near the beginning of January. However, since juveniles up to 60 mm ML were caught at the same time, a protracted spawning period is indicated. Using a growth curve combining the above data as well as published values of increment counts of juveniles, spawning of these larger animals can be estimated to have been as much as 100 days earlier. The mixing resulting from the complex oceanographic regime of the frontal zone along the inshore edge of the Gulf Stream off Florida, where both larvae and juveniles were concentrated (Rowell & Trites. 1985 *Vie Milieu*. 35: In Press), could account for the simultaneous presence of such diverse age groups in one location. These observations support the thesis that the spawning season is a prolonged one, and the spawning area widespread, possibly from the Gulf of Mexico to east of Cape Hatteras.

LABORATORY CULTURE OF *OCTOPUS DOFLEINI* FROM HATCHING TO SETTLEMENT.

S. Snyder. The Seattle Aquarium, Washington.

Captive spawned *Octopus dofleini martini* were reared from hatching to settlement. Hatching occurred 5-6 months after laying, at an incubation temperature range of 9.4 to 13.0°C; the nektonic hatchlings measured 6-8 mm total length. Growth and settlement were very gradual; settlement was not definitive until 7-8 months of age, at a size of approximately 30 mm total length. Maximum losses occurred during the first month -- from an initial number of 564, 158 hatchlings remained; 25 remained at 6-7 months of age. One remained by 8-9 months of age, surviving to adulthood. Periodic bacterial infections were the primary cause of death and were treated with a variety of antibiotics. The culture vessel was small-scale (24 *l*), circular, and open system, at ambient salinity (26.5-29.5 $^0/_{00}$). Temperature, flow rate, and lighting were controlled throughout development. Several types of freshly killed or frozen foods proved to be readily acceptable; no live plankton was used.

GONATID SQUIDS AS PREY FOR SALMONIDS AND OTHER TOP CARNIVORES IN THE SUBARCTIC PACIFIC.

W. G. Pearcy and **K. Jefferts,** College of Oceanography, Oregon State University, Corvallis.

Gonatid squids are important prey for several species of epipelagic carnivores caught in drift gill nets during the summer in the eastern subarctic Pacific. *Gonatus middendorfi* is common in salmon stomachs in the northern Gulf of Alaska. *Berryteuthis anonychus* is often the single most important prey species for salmonids, pomfret and *Ommastrephes bartrami* in the region of the Subarctic Current where it accounts for many full stomachs and appears to be a key prey species.

ASPECTS OF DISPLAYING LIVE CEPHALOPODS.

Roland Anderson, The Seattle Aquarium, Washington.

The Seattle Aquarium regularly displays *Octopus dofleini* and *O. rubescens* along with a sepiolid, *Rossia pacifica*. In addition to these local species *Nautilus pompilius* is displayed in a tropical gallery. *Loligo opalescens* is displayed seasonally and *Sepia officianalis* has been displayed as space and supply of the animal have been available. Three other cephalopods have been kept in non-display tanks. Exhibiting these animals for public display is usually a challenge. The Aquarium has used some interesting methods for presenting these cephalopods to the public, solutions that keep the animals healthy yet available for viewing by literally thousands of people. Methods include use of an acclimation period in a holding tank, where the animal gets used to the conditions of confinement. The process of confining an octopus can be a challenge in itself, which is met by suitably enclosing the holding and display tank. While on display the animal is provided a natural appearing habitat, such as artificial caves or substrate, that also lets the animal be visible to the public. Red light, low-level lighting, mylar coatings on the glass and one-way mirrors have been tried to reduced animal stress. Water quality and food quality is closely monitored. Some of the cephalopods have reproduced while on display, indicating good adjustment to captivity.

MOROTEUTHIS OF MONTEREY: HATCHLINGS THROUGH ADULTS.

W. F. Gilly, F. Horrigan and **N. Fraley.** Hopkins Marine Station of Stanford University, Pacific Grove, California.

Mature specimens (both sexes up to 1 m d.m.l.) of genus *Moroteuthis* were regularly obtained during 1985-86 as incidental catch by bottom trawlers at 100 fathoms in sandy areas associated with local submarine canyons. During September 1985 we also obtained juveniles (approx. 5 cm d.m.l.) from stomach contents of freshly (sport) caught albacore (*Thunnus alalunga*) and hatchlings (less than 5 mm d.m.l.) from surface plankton tows, both from the same general area where adults were taken. We hypothesize that *Moroteuthis* spawns locally in these areas.

Taxonomic status of the local specimens is vague. Although the large adult size and mantle texture suggest *M. robusta*, arm length indices are distinctly shorter than those for that species. Numbers of tentacular carpal pads/suckers (11-13) and paired hooks (no more than 16) identify our specimens with *M. pacifica*, which has recently been described from only small specimens (less than 16 cm d.m.l.) Fin width indices of juvenile Monterey specimens match *M. pacifica* (greater than 0.50), but those of adults match *M. robusta* (less than 0.50). Sexual dimorphism exists in our adults; males have a prominent fleshy keel on the ventralmost (IV) arms that the females lack.

We have also carried out histological studies of the nervous systems in adults. Stellate ganglia with all stellar nerves attached were fixed, embedded, and sectioned at 2 microns. Each nerve contains a large number of small (0.5 -10 micron dia.) axons and up to 12 larger axons ranging to 150 micron dia. *Moroteuthis* thus does have 'giant' axons that presumably control jetting by the very muscular mantle.

LIFE HISTORY ASPECTS OF *OCTOPUS BIMACULOIDES* IN A COASTAL LAGOON.

M. A. Lang. Department of Biology, San Diego State University, California.

Agua Hedionda lagoon in Carlsbad, California is a shallow water coastal lagoon, with oceanic, not estuarine conditions due to excellent flushing during tidal changes. The lagoon supports an unusually high density of *Octopus bimaculoides*. The sampling design of this study consists of two grids, each covering an area of 25m x 22m. Twelve 25m long parallel transect lines contain 25 octopus traps each, spaced at 1m intervals. Each transect line is anchored to the sand bottom at approx. 8m depth and at 2m distance from its neighboring transect. The two grids are placed 50m apart. The octopus traps consist of aluminum cans with 1/6 of their volume removed and fasteners of easy removal from the grid. *Octopus bimaculoides* are sampled monthly. The octopuses are anaesthetized in 3% ethanol in seawater, mantle caps are inverted, sexes, weights and measurements are taken, and a numbered fingerling tag is permanently affixed to the inside of the mantle cavity. Octopuses are then released at the center of each grid and allowed to randomly redistribute. Censuses using SCUBA are done to determine small-scale movement within the grids as well as trap occupancy, at times amounting to 1/3 of the traps being occupied. The bottom is very shelter-limited, therefore the rapid inhabitation of the available cans as dens. Females will readily brood eggs in the traps on a year-round basis, with brood sizes ranging from 266-776 eggs. Hatchlings are benthic, and weigh approximately 70 mg, with a 7 mm dorsal mantle length. Abundant schools of mysids and larval fishes are present throughout the year. The major prey item of juveniles and adults is the speckeled bay scallop *Argopecten aequisulcatus* which, as the octopus population, is unusually high in numbers. Scallops are either drilled or pulled apart. Other prey species recovered from the traps include *Crucibulum spinosum Crepidula onyx, Semele decisa, Saxidomus nuttalli, Laevicardium substriatum* and various small crustacea. Reproduction and brooding is observable on a year-round basis. Mature males and females will mate readily in the laboratory. In the lagoon, a 1:1 sex ratio is encountered. Major predators of these octopods are halibut, rays, and other octopuses. Large *Octopus bimaculatus*, a sibling species, have been found on 16 occasions. Their planktonic early life history trait provides a mechanism by which they can be flushed into or out of the lagoon, making it highly unlikely that they could remain in the lagoon until settlement.

ABSTRACTS
MOLLUSCAN MORPHOLOGICAL ANALYSIS SYMPOSIUM

Organized by D. R. Lindberg and C. S. Hickman
University of California Berkeley

MOLLUSCAN MORPHOLOGICAL ANALYSIS SYMPOSIUM; OPENING REMARKS. Carole S. Hickman. Department of Paleontology, University of California, Berkeley.

The analysis of form is essential to the understanding of any group of organisms. In malacology we use a variety of techniques of morphological analysis to characterize and describe new taxa, to compare taxa, to classify taxa, and to evaluate phylogenetic relationships. We analyze form in order to understand function and to evaluate performance. The analysis of form is central to understanding molluscan development. And the analysis of form is essential to defining on one hand the intrinsic properties of molluscan structure and on the other hand the theoretical possibilities for creating molluscan novelty — the limits of molluscan evolutionary potential.

This symposium focuses on a diversity of opportunities to understand molluscan form and structure, including those that exist outside traditional systematic framework. It emphasizes relatively new methods and techniques and their application to the resolution of specific problems.

A brief review of the great traditions and philosophical approaches to the analysis of morphology shows that Malacology has a long-established great tradition in "functional anatomy". Its strengths are the elegant manner in which it has used the comparative method and the manner in which it has examined form in the contexts of function and ecology. It is a tradition that is rooted in natural history in the best sense of the word and a tradition that has illuminated the basic biology of mollusks. Other powerful traditions that have developed outside of malacology (particularly those developed by paleontologists and vertebrate biologists) are applicable to molluscan problems but are under-appreciated by malacologists. The traditions of theoretical morphology, biomechanics, and constructional morphology provide some of the best examples of the specific techniques and approaches that are developed in the symposium.

A MODEL FOR SHELL PATTERNS BASED ON NEURAL ACTIVITY. John H. Campbell, Department of Anatomy, University of California, Los Angeles.

The patterns of pigment on the shells of mollusks provide one of the most beautiful and complex examples of animal decoration. Recent evidence suggests that these patterns can arise from the stimulation of secretory cells in the mantle by the activity of the animal's central nervous system. A mathematical model based on this notion has been developed. A rather simple scheme of nervous activation and inhibition of secretory activity can reproduce a large number of the observed shell patterns.

PHYSICAL DETERMINANTS OF SHELL SHAPE IN LIMPETS. M. W. Denny, Stanford University, Hopkins Marine Station, Pacific Grove, California.

The optimum shape of a limpet's shell is determined by both biological factors (eg. the need for a "plow" in the aggressive territorial limpet *Lottia gigantea*) and physical factors (eg. the need to minimize force, desiccation or heat load). It is proposed that the optimum shape determined by physical factors alone sets the "theme" upon which individual species have evolved variations due to biological selective pressures. It is suggested that the physically optimum shape can be largely determined by fluid dynamic forces, minimizing the risk of a limpet being dislodged. This shape represents a trade-off between drag (the primary force in the direction of flow) and lift (the force perpendicular to flow). Measurements using cones as models of limpets show that flattened shells (height/diameter small) have a low drag but a high lift. Highly peaked shells (height/diameter large) have a large drag but low lift. A cone with height/diameter = 0.7 minimizes the net imposed force per body volume. Shells with an apex located anterior of center have a high lift when the apex is upstream and a low lift when the apex is downstream. However, in most intertidal habitats the direction of flow is unpredictable, precluding the possibility that a limpet can reliably orient its anterior end downstream, and as a result a shell with a centrally-located apex experiences the lowest maximum lift. Thus on the basis of fluid-dynamic considerations, it is proposed that the optimum limpet-shell shape is a cone with a central apex and a height to diameter ratio of approximately 0.7. This prediction is a reasonable approximation of shells found in nature. Examples of divergence due to biological factors and the complicating effects of desiccation resistence and heat transfer are discussed.

UNRAVELING THE GASTROPOD PEDAL MUSCULATURE FABRIC: PATTERNS OF MORPHOLOGY AND LOCOMOTION. Janice Voltzow, Friday Harbor Laboratories, Washington.

The gastropod foot is a fleshy, flexible organ that performs a diversity of functions. Despite its importance to the animal, the functional morphology of the foot has traditionally been overlooked. Information about the foot can lead to furthering our understanding of gastropod phylogeny, locomotor mechanics, reproductive and other life history traits, and the fossil record, as well as serving as a model system for connective tissue-mediated muscle-muscle interactions. An orderly, multi-level progression of microscopic and reconstruction techniques reveals that the seemingly random set of muscle fibers within the foot has distinct regions, the columellar muscle and tarsos, with recognizable features. These general features form a basis of comparison between species.

One application of this technique has uncovered the morphological differences underlying the functionally distinct monotaxic and ditaxic waves of the limpet foot. This discovery has led to the reconstruction of the foot of monoplacophorans and the prediction of their locomotor wave type.

ARIZONA HYDROBIIDAE: SYSTEMATICS AND MORPHOMETRICS. R. Hershler, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

In a systematic study of Arizona spring snails, genus *Fontelicella* (Hydrobiidae), 12 allopatric species were recognized. Stepwise discriminant analysis was used to test whether these species can be separated on the basis of the type of data sets often used by hydrobiid systematists, and to examine patterns of variation. Regardless of whether shell or anatomical data were used, over 88% of topotypical specimens were correctly classified in discriminant analyses, suggesting that these data can successfully distinguish between purported species. Classification of individuals from additional localities was not as satisfactory, indicating that inter-population variation is often significant and that larger sample sizes may be needed. Shell variables did not separate the species as well as anatomical variables did, and penial features proved most useful in this regard, as this structure is relatively variable among these species compared to other anatomical aspects or shell.

MULTIVARIATE ANALYSIS OF CHITON VALVE MORPHOLOGY. Douglas J. Eernisse, Friday Harbor Laboratories, Washington.

A variety of multivariate methods were used for intra- and interspecific comparisons of valve morphology in the chiton genus *Lepidochitona*. Specific applications of morphometric techniques are presented, using data sets of digitized homologous landmarks. For examining variation within a population, replicated measurements were taken of both the left and right sides of valves 5 and 8 from a collection of 60 *L. dentiens* (Gould, 1846) from San Juan Island, Washington. After transforming the data to remove size effects, A 2-way mixed-model ANOVA was performed to estimate variance due to i) directional asymmetry around a bilateral axis, ii) non-directional asymmetry. For most measurements compared, both directional (favoring the animal's right side) and non-directional asymmetry were found to be significantly greater than expected due to measurement error or random effects alone. Chitons may not be as perfectly bilaterally symmetrical as initially presumed and, individuals differ in observed levels of asymmetry.

As examples of interspecific shape comparisons, data from one side of valve 5 were compared among as many as nine *Lepidochitona* spp., as well as two species in other genera used for outgroup comparisons. A combination of principal component and canonical discriminant analyses of covariance matrices was used. Altogether, 231 animals were collected from different populations in each species' range, and using a variety of morphological and biochemical characters independent of valve shape, were assigned with confidence to a particular species for discriminant analysis. Discrimination between each species was consistently high, and approximately 95 percent of the individuals were classified to the correct group based on comparison of their individual discriminant scores to each group's centroid. Principal component analysis was generally more useful for factoring out size and shape factors with no a priori assumptions concerning group assignment, and indicated that the observed variation among even the most morphologically similar species was due, at least in part, to shape differences.

GASTROPOD GUT AND RADULA MORPHOLOGY: EVOLUTIONARY IMPLICATIONS OF A MICROCOMPUTER ASSISTED STUDY. David R. Lindberg, Museum of Paleontology, University of California, Berkeley.

The coiling and looping patterns of the gastropod gut and radula, and the numerous character states associated with the radula have been often used to infer relationship between taxa. Results and observations from three current research projects that use characters from the molluscan alimentary system and microcomputer-based analyses are discussed: (1) the construction of phylogenetic hypotheses using phylogenetic inference software (CLINCH, PAUP, PHYLIP), (2) the identification of heterochronic changes in the patellogastropod alimentary system and the use of computer-assisted drawing (CAD) software for anatomical reconstructions, and (3) microcomputer modeling of radular morphology based on the patterns of odontoblast and tooth formation in prosobranch mollusks. Determining the polarity of anatomical characters for phylogenetic analysis can be complicated by the presence of heterochrony in certain organ systems, and can lead to confusion of derived (recapitulated) characters with primitive ones. Moreover, false pleisomorphies are suggested when workers only use characters from the adult mollusk rather then consider the complete ontogeny. For example, both an operculum and epipodial tentacles are present in larval patellogastropods, but the characters are typically scored as absent in this taxon because they are not present in the adult. The alimentary systems of the patellogastropods show increasing juvenilization as one moves from the ancestral to derived taxa. This includes fewer loops of the gut and fewer radular teeth. Because the radular sac buds off the stomodaeum early in development, these two compatible character states can be developmentally linked. Patterns of heterochrony in radular morphology were modeled by assuming one tooth per odontoblast, the existence of a single primordial odontoblast, three fields of radular teeth, and simple cell division followed by differentiation based on positional information. All extant radular patterns can be generated by this model using simple assembly rules. Using random variables to determine the number and presence or absence of cell divisions and tooth placement, the ancestral prosobranch radular morphologies (docoglossate, rhipidoglossate) occur with significantly less frequency then the derived types (rachiglossate, taenoglossate).

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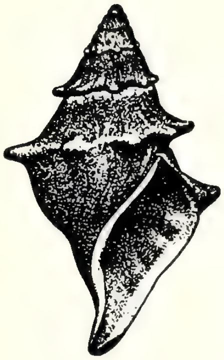

With the publication of *PERSPECTIVES IN MALACOLOGY* (July 1985), the *AMERICAN MALACOLOGICAL BULLETIN* has taken its first step in producing important and timely special publications of malacological interest. *PERSPECTIVES* offers a wide range of papers dealing with various aspects of molluscan biology of interest to professional and amateur malacologists alike. These papers were presented as part of a symposium held in honor of Professor M.R. Carriker and highlight many recent advances in many facets of the study of molluscs. *PERSPECTIVES IN MALACOLOGY* offers insight into some frontiers of molluscan biology ranging from deep-sea vent malacofauna to chemical ecology of oyster drills.

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Seed, R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms*, D. C. Rhoads and R. A. Lutz, eds. pp. 23-67. Plenum Press, New York.

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Cover. *Strombus gigas* Linné is an ecologically and economically important component of the malacofauna of the Caribbean and the symbol for the 1987 annual meeting of the American Malacological Union (see page 151, this volume, for meeting information).

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HABITAT ECOLOGY OF JUVENILE FRESHWATER MUSSELS (BIVALVIA: UNIONIDAE) IN A HEADWATER STREAM IN VIRGINIA

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ABSTRACT

The occurrence and distribution of juvenile freshwater mussels (ages 0-3 years) were assessed at a site on Big Moccasin Creek, southwestern Virginia, between January 1983 and March 1984. A circular bucket sampler (573 cm^2) with a 130 μm mesh bag net was used to collect 91 qualitative and quantitative samples from various habitats in the stream. A total of 92 juvenile mussels was collected; densities were greatest behind boulders and numbers were greatest in riffles and runs. Juveniles were decidedly clumped in distribution, and their occurrence was significantly correlated with the occurrence of fingernail clams. Most older juveniles (ages 2 and 3 years) occupied habitats similar to those inhabited by adults. The relatively high mean annual mortality of juveniles (approximately 44%), their low abundance, and the many age classes in each mussel population in Big Moccasin Creek appeared to indicate that low but relatively stable recruitment each year was sufficient to maintain a viable mussel assemblage in the stream.

The glochidia of freshwater mussels are obligate parasites on the gills or fins of fish, and if attachment to a suitable fish host occurs, the glochidia encyst, metamorphose, and excyst to begin their free-living stage as juveniles (sexually immature mussels) in the stream or lake bottom. Mortalities during this unique life cycle are believed to be greatest at two stages; unsuccessful attachment to the appropriate fish host and dropping from the fish into an unsuitable habitat. Contact with a fish host and the place of shedding young mussels from the host are largely due to chance, and only the juveniles that reach a favorable habitat survive (Howard, 1922). The presence of a byssus in juveniles of some species apparently serves for attachment to and stability in the substratum (Frierson, 1905). Although early investigators of mussel life histories recommended research on the juvenile stage (Coker *et al.*, 1921), no such studies were conducted.

The location and habitat of juvenile mussels have been enigmas to malacologists, particularly in lotic systems. As in many taxa of aquatic fauna, conditions favorable for the juvenile stage can differ from those favorable for adults. Coker *et al.* (1921) noted that the study of habits and habitats of juveniles was difficult because the small mussels had rarely been collected. The juvenile shell up to 2 months of age is small (<1 mm long), transparent, and not calcareous (Howard, 1917); locating such specimens in a stream or river bottom is therefore difficult. Lefevre and Curtis (1912) reported that the juvenile period immediately following parasitism (lasting until approximately 20 mm in shell length) was the least known and least collected; later studies confirmed these early observations (Negus, 1966; Ahlstedt, 1979; Neves *et al.*, 1980).

With twenty-three species of freshwater mussels included in the federal list of endangered species, and designations of critical habitat in their respective recovery plans, the collection of new information on juvenile habitat and ecology is obviously critical. Casual observations and incidental data available on the juvenile stage are no longer sufficient to provide for the protection and enhancement of these and other declining populations of mussel species in the United States. Therefore, the objectives of this study were to locate juvenile mussels in a headwater stream and to describe the habitats used in this life history stage.

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MATERIALS AND METHODS

Big Moccasin Creek (BMC) is a third-order stream flowing 88 km through Scott and Russell counties in southwestern Virginia and entering the North Fork Holston River near Weber City, Virginia. The study site (36°47'30''N, 83°11'50''W) is near the intersection of State Routes 676 and 677 (Owen's Farm) in Russell County. There the stream flows through open pasture; width and depth average 7.0 m and 0.2 m, respectively, during low flow conditions. Substratum composition is coarse particle sizes in runs and riffles, with sand and silt in pools. Water chemistry and temperature data for BMC were presented by Zale and Neves (1982a). This site was selected for study because the stream here is relatively small, easily accessible, and has a dense mussel assemblage consisting of seven mussel species: *Medionidus conradicus* (Lea), *Villosa nebulosa* (Conrad), *V. vanuxemi* (Lea), *Pleurobema oviforme* (Conrad), *Fusconaia barnesiana* (Lea), *Lampsilis fasciola* Rafinesque, and *Alasmidonta viridis* Rafinesque (Weaver, 1981; Neves and Zale, 1982; Zale and Neves, 1982b). The Asiatic clam, *Corbicula fluminea* (Müller, 1774), does not occur in upper BMC. Since a previous study in BMC indicated that mussels less than four years old were not sexually mature (Zale, 1980), we defined the juvenile stage as consisting of mussels of ages 0 to 3 years.

Three major habitat types (pool, run, and riffle) were identified for sampling. Pools were characterized by slow flow, greater water depth, and an overlying layer of silt on the stream bottom; runs had moderate current velocities, laminar flow, intermediate depths, and coarse substrata; and riffles had swift, turbulent flow, shallow depths, and coarse substrata. Two microhabitats were identified for sampling in these habitat types; the downstream side of boulders in the stream bed, and the area along stream banks.

In January and March 1983, initial qualitative samples of substratum were collected at the site to test the feasibility of sampling methods. An engine-driven centrifugal pump was tried but quickly became clogged by coarse substrata. Efforts to collect substratum samples with a vertical corer 5 cm in diameter were also unsuccessful because of the coarseness of subsurface substrata. All subsequent sampling for juvenile mussels was done with a circular (573 cm^2) bucket sampler with a removable 130 μm mesh nylon bag net attached to its downstream side. The sampler was pushed into the stream bottom, and all substratum was scraped into the net by hand and hand cultivator to the greatest depth possible. Each sample was emptied into a 13*l* plastic bucket and fixed with 5% buffered formalin. We collected 16 preliminary samples of substratum from various habitats in the stream to determine whether juveniles could be located, and where subsequent sampling effort should be directed.

A systematic sampling design was used in each of the three major habitats. Three substratum samples were taken along transects in each habitat on 6 May, 7 June, 14 July, 12 September, and 28 October 1983. A total of 45 samples (3 samples from five transects in each habitat) were collected. Three samples from each microhabitat (behind boulders, along banks) also were collected on the following dates: 12 September and 17 December 1983; and 30 January, 5 March, and 23 March 1984. Because core sampling was not possible, we stratified microhabitat samples by depth. The upper layer of loose substratum was collected, and then using a hand cultivator to loosen the lower layer, as much of the remaining substratum as possible was removed separately. Sampling in BMC was limited to depths of about 15 cm because the deeper substratum was hardpan. Each layer was preserved and stored for later examination. Measurements taken concurrently with each substratum sample included water depth, and surface and bottom water velocity (with a pigmy current meter).

In the laboratory, each of the 75 quantitative samples was washed through a series of three U.S. Standard Sieves (6.5 mm, 2.0 mm, 125 μm), sorted, and classified according to a modified Wentworth scale as follows (Hynes, 1970): cobble, 64-256 mm; pebble, 6-63 mm; gravel, 2-5 mm; sand, 0.06-1 mm; and silt, <0.06 mm. Cobble and pebble fractions of substratum samples were visually inspected for juveniles, and gravel and sand fractions were examined under a dissecting microscope at 12X magnification. Previous studies showed that no juveniles passed through the 125 μm sieve (Zale and Neves, 1982b); consequently, the silt fraction was not inspected. Processing of each sample required 1 to 5 days, depending on the quantity and composition of substratum.

All juvenile mussels and fingernail clams (Sphaeriidae) were removed, counted, and placed in vials of 10% buffered formalin. Adult mussels in each sample were identified and counted. Cobble and pebble substratum fractions were air-dried; gravel, sand, and silt components were oven-dried at 100°C for 48 hrs. Each dried fraction was weighed on a triple beam balance to determine particle size composition, by weight, of each sample. Densities of juvenile mussels and sphaeriids were computed per sample and converted to numbers per square meter of substratum sampled. Juveniles were aged in years by counting growth rings on the external surface of valves and tentatively identified to genus by comparing the umbonal beak sculpture with that on the shells of adult mussels from the study site. Shell lengths and widths of juveniles were measured with vernier calipers or with an ocular micrometer under a dissecting microscope.

Kruskal-Wallis one-way analysis of variance was used to determine whether mollusc abundance differed significantly among habitat types. Two dependent variables, juvenile mussel and sphaeriid densities, were tested against water depth, surface and bottom current velocity, and percent cobble, pebble, gravel, sand, and silt. Spearman rank correlations were used to determine relationships between densities of juvenile mussels, fingernail clams, and measured physical variables (Zar, 1974).

To obtain an estimate of the number of juvenile mussels in this 100 m section of BMC, the site was physically surveyed by transects, mapped, and categorized into the five habitat types on the basis of stream bottom areas measured.

Using the area-density method, we multiplied mean densities of juveniles in each habitat type by total area of that type to estimate abundance (Everhart *et al.*, 1975). Numbers per habitat type were summed to estimate total number of juveniles. A survival estimate of juveniles of all species combined was calculated using the relative abundance of each juvenile cohort (ages 0-3 years) in the 75 quantitative samples, according to the Robson and Chapman method (Ricker, 1975).

RESULTS

We collected 17 juvenile mussels in the 16 preliminary samples. Sphaeriids were common in all samples but juvenile mussels occurred only in samples from riffles and runs. Later quantitative samples collected from March 1983 to March 1984 differed in the occurrence of juveniles among habitat types, although some were taken in all habitats sampled. Totals of 75 juvenile and 36 adult mussels were collected in the 75 quantitative samples taken on the nine sampling dates (Table 1). Juveniles were present in only 30 of the 75 samples and were clumped in distribution (Fig. 1). For example, 18 of the juveniles taken behind boulders were in 2 of the 15 samples from this microhabitat.

Sphaeriids were relatively common in all samples and occurred, in order of decreasing abundance, in the pool, runs, behind boulders, along banks, and riffle habitats. Three species of fingernail clams were identified: *Pisidium compressum* Prime, *P. casertanum* (Poli), and *Sphaerium striatinum* (Lamarck). A clumped distribution of sphaeriids was also evident but no distributional analysis by species among habitat types was attempted.

Table 1. Number, age group, and location of mussels collected in 75 quantitative samples from Big Moccasin Creek on nine sampling dates, May 1983 to March 1984.

HABITAT	JUVENILE AGE GROUPS (yrs)					ADULTS	TOTAL
	0	1	2	3	Total Juveniles	≥4	
Pool	0	4	3	1	8	0	8
Run	4	3	3	1	12	7	19
Riffle	5	6	3	3	17	13	30
Boulder	15	6	7	7	35	8	43
Bank	1	1	0	1	3	8	11
TOTAL	25	20	16	14	75	36	111

Because juvenile mussels and sphaeriids showed a clustered distribution, and sampling covered only a small fraction of total habitat, our computed estimates of bivalve densities are considered to be only rough approximations (Table 2). Densities (no./m^2) based on sampling results ranged from 0 to 52 juveniles in riffles, pools, and runs; 0 to 17 along stream banks; and 0 to 175 behind boulders. The wide ranges reflect the apparently clustered distribution of this life history stage.

Of the 92 juvenile mussels collected in qualitative and quantitative samples from BMC, 69 were less than 15 mm long (range 0.8 - 30.3 mm). Identifications were as follows: 50 *Villosa* spp., 34 *Medionidus conradicus* and 8 *Fusconaia barnesiana* or *Pleurobema oviforme*. Four age classes (0-3) were identified, with slightly more specimens in age classes 0 and 1 (Table 3). Mean lengths of juveniles ranged from 2.7 mm for age 0 to 23.2 mm for age 3. Age 0 individuals were most commonly collected behind boulders and were absent

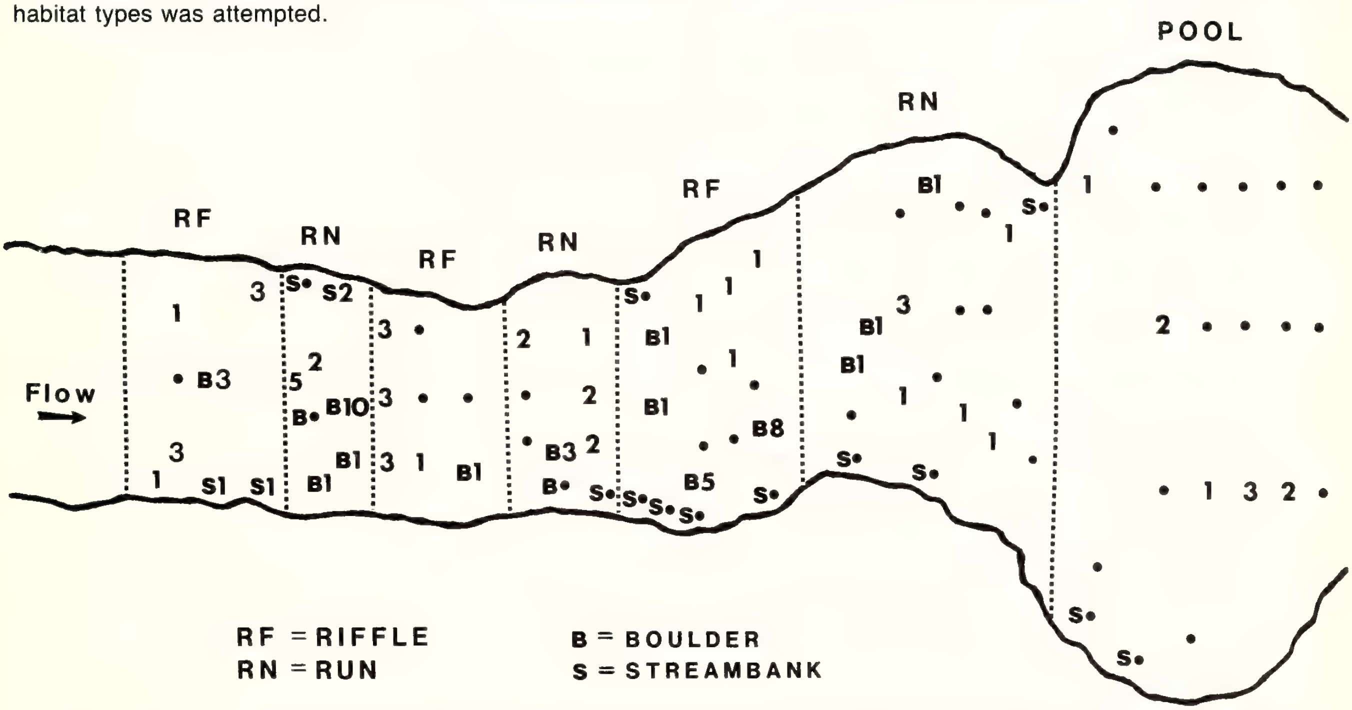

Fig. 1. Location of samples, and the number and location of juvenile freshwater mussels collected at the study site in Big Moccasin Creek. Numbers indicate number of juveniles collected at that location; ● represents sample locations without juveniles; S and B identify microhabitat samples along streambanks and behind boulders, respectively.

Table 2. Number and weighed mean densities (no./m²) of juvenile mussels and fingernail clams in 75 quantitative samples from Big Moccasin Creek on nine sampling dates, May 1983 to March 1984.

HABITAT	JUVENILE MUSSELS No.	JUVENILE MUSSELS Density	SPHAERIIDS No.	SPHAERIIDS Density
Pool	8	9.3	1046	1218
Run	12	15.1	616	717
Riffle	17	25.6	162	189
Boulder	35	39.6	570	664
Bank	3	2.3	478	557

Table 3. Cohorts and sizes of all juvenile mussels collected in Big Moccasin Creek, May 1983 to March 1984.

AGE	NO.	SHELL LENGTH (mm) mean	SHELL LENGTH (mm) range	SHELL LENGTH (mm) SD	SHELL WIDTH (mm) mean	SHELL WIDTH (mm) range	SHELL WIDTH (mm) SD
0	27	2.7	0.8-5.0	1.22	1.8	0.6-3.4	0.80
1	25	6.4	2.2-11.0	2.32	3.6	1.6-5.4	1.05
2	20	13.6	4.5-21.2	3.82	7.8	2.9-12.9	2.29
3	20	23.2	11.2-30.3	5.68	12.9	5.7-17.2	2.71

in the pool samples. Adult mussels, which occurred most frequently in riffle samples, were also absent in the pool (Table 1); however, some adults were seen in pools during low flow conditions. A relatively wide size range within cohorts, most evident in ages 2 and 3, was attributed to differences in species and growth rates. One specimen 25.7 mm long (age 3) was gravid but was nevertheless included in the juvenile category because eight larger juveniles ($>$ 25 mm shell length) were immature. Mean annual survival for juveniles, as determined by the Robson-Chapman method, was 56% for ages 0 to 3 years. This estimate of juvenile mortality (44% per year) excludes the high mortality reported to occur within a few days after mussels drop from the fish host.

Occurrence of juvenile mussels behind boulders in the stream was most often in the upper stratum of samples (0-8 cm deep). Of the 26 juveniles collected in these quantitative samples, 20 were in the surface layer.

Differences in densities of juveniles among the five habitat types, statistically analyzed with a Kruskal-Wallis test, were significant ($p = 0.01$). Because of the large number of samples that contained no juveniles (45 of 75), a chi-square contingency test was used to corroborate results of the Kruskal-Wallis test. Chi-square analysis confirmed that juvenile densities were significantly different among habitat types ($\chi^2 = 44.3$; $p < 0.001$). Multiple comparison tests made with these mean density data indicated that the density of juveniles behind boulders was significantly greater than that in pool habitat ($p = 0.009$) or along banks ($p = 0.001$), and significantly lower along stream banks than in riffles or runs ($p = 0.02$).

Kruskal-Wallis tests ($p = 0.05$) used to compare bivalve densities and environmental variables also revealed significant associations (Table 4). Multiple comparison tests between juvenile mussel abundance and the five habitat types indicated significant differences between the following: pool and boulder, run and bank, riffle and bank, and boulder and bank. These four paired comparisons also differed significantly in bottom and surface current velocities, indicating that the occurrence of juvenile mussels was correlated with water velocity in these habitats. Comparable tests with fingernail clam data showed significant differences between pool and riffle, run and riffle, and riffle and boulder habitats. No consistent trends between bivalve densities and substratum type were evident.

Spearman rank correlation tests between juvenile mussel densities and other measured variables indicated a significant association only with sphaeriid densities ($p = 0.05$). Areas in the stream with the most juvenile mussels also had the most sphaeriids. These correlation tests were influenced to a considerable degree by the relatively small numbers of juveniles and the many samples from all habitats that included no juveniles. Because of these two factors, sensitivity of the statistical tests is considered low.

As judged by the density of juvenile mussels and fingernail clams in each habitat and the total areas of those habitats, approximately 11,000 juvenile mussels and 582,000 fingernail clams occurred within our 100 m section of BMC (Table 5). Although juveniles were in greatest density behind boulders in riffles and runs, this habitat type composed only 0.9% of the stream bottom and supported less than 3% of

Table 4. Summary of habitat data, mean and range (in parentheses), collected with quantitative samples from Big Moccasin Creek, May 1983 - March 1984.

HABITAT	WATER DEPTH (cm)	VELOCITY (cm/s) Surface	VELOCITY (cm/s) Bottom	SUBSTRATUM (%) Cobble	SUBSTRATUM (%) Pebble	SUBSTRATUM (%) Gravel	SUBSTRATUM (%) Sand	SUBSTRATUM (%) Silt
Pool	25 (14-40)	5 (0-36)	4 (0-17)	6 (0-23)	53 (45-63)	20 (11-31)	21 (9-28)	<1 (0-2)
Run	22 (12-31)	20 (3-53)	12 (0-30)	31 (4-61)	49 (31-64)	11 (2-24)	9 (1-13)	<1 (0-1)
Riffle	19 (7-32)	36 (6-78)	33 (6-78)	33 (12-49)	50 (39-62)	10 (3-19)	7 (2-16)	<1 (0-2)
Boulder	24 (7-38)	32 (0-92)	32 (0-92)	34 (0-71)	43 (23-64)	12 (2-28)	11 (4-25)	<1 (0-1)
Bank	28 (6-39)	10 (0-49)	10 (0-70)	23 (22-67)	52 (2-23)	11 (4-28)	13 (0-2)	<1

the total estimated juveniles present. A total of 8139 (75%) of the 10,830 juveniles at the site were in riffles and runs, which together accounted for roughly 55% of the stream bottom area. Juvenile densities were lowest along the stream banks and in pools, but the relatively large area of pool habitat (28.1%) accounted for 19% of the total juveniles.

Table 5. Estimates of juvenile mussel and fingernail clam abundance at the study site (100 m long) in Big Moccasin Creek, based on the area-density method.

HABITAT TYPE	AREA (m^2)	PERCENT AREA	MUSSELS (no./m^2)	MUSSELS Total	CLAMS (no./m^2)	CLAMS Total
Run	283	35.6	15.1	4273	717.1	202,939
Riffle	151	19.0	25.6	3866	188.6	28,479
Pool	224	28.1	9.3	2083	1217.7	272,765
Boulder	8	0.9	39.6	309	663.6	5,309
Bank	130	16.4	2.3	299	556.5	72,345
TOTAL	796	100.0	-	10,830	-	581,837

DISCUSSION

The contagious distribution of juvenile mussels among habitats and samples within habitats in BMC accounted in part for the difficulty in locating juveniles, as described in earlier studies (Isely, 1911; Coker *et al.*, 1921). Our results and those of previous studies in rivers concur in juvenile habitat description; namely, swift water with substrates of coarse gravel and boulder. Early investigators consistently reported the occurrence of a byssal thread on juvenile mussels, first observed after about 38 days (Isely, 1911; Howard, 1922). In Oklahoma rivers, Isley (1911) found juveniles attached to rocks and pebbles where water currents were swift. We observed few juveniles with a byssus, but because of the methods used to obtain and process substrate samples, byssal threads extruded by juveniles were probably broken.

The relatively high abundance of age 0 mussels behind boulders in riffles and runs has not been previously reported. The tendency of currents in streams to deposit finer particulate and organic matter in the eddies behind boulders, may account for their greater occurrence at these locations. Except for typically smaller particle sizes in the surface layer of substrate behind boulders, the overall composition of substratum down to roughly 15 cm was similar to that in other habitats. Since most of the juveniles were in the upper portion of substratum (0-8 cm), environmental conditions in this unconsolidated substratum were presumably suitable for young mussels.

The habitat for juvenile mussels in lotic systems differs from that reported for lakes. Juveniles of lake species have been collected primarily in sandy substrata (Coker *et al.*, 1921; James, 1985). Ecological adaptations, even at the juvenile stage, can exist between lotic and lentic species, as well as among lotic species in headwater streams versus large rivers. Just as adults of many mussel species exhibit non-random distributions in response to environmental conditions, we suspect that subtle microhabitat preferences also occur among juveniles of at least some species. However, information on this early life stage is inadequate to enable us to judge whether the distribution of juveniles in BMC was due to differential survival among habitat types, habitat preference, or excystment of newly metamorphosed juveniles from host fish into those habitats.

Natural mortality appears to be high during the first year of life, since Howard (1922) reported a scarcity of young mussels even a few days after metamorphosis. Predators such as turbellarians and fishes take their toll, but the greatest natural mortality is believed to result from the mussels falling into unfavorable habitat or from the effects of spates on settled juveniles (Coker *et al.*, 1921). Microhabitat preferences of stream fishes are well documented (Gorman and Karr, 1978; Gatz, 1979), and the following species serve as hosts for the dominent mussel species in BMC (Weaver, 1981; Zale and Neves, 1982b): smallmouth bass (*Micropterus dolomieui* Lacépède), rock bass (*Ambloplites rupestris* Rafinesque), banded sculpin [*Cottus carolinae* (Gill)], redline darter [*Etheostoma rufilineatum* (Cope)], fantail darter (*E. flabellare* Rafinesque), central stoneroller [*Campostoma anomalum* (Rafinesque)], river chub [*Nocomis micropogon* (Cope)], war paint shiner [*Notropis coccogenis* (Cope)], and whitetail shiner [*N. galacturus* (Cope)]. Since most of these species are considered to be riffle-dwellers, newly metamorphosed mussels would likely be dropped into riffles. The correlation between density of juveniles and water velocity tends to support this observation. Howard (1922) reported that young mussels, in suitable substratum and undisturbed, seemed to be relatively inactive. If these early observations are correct, the juveniles collected behind boulders and in riffles in BMC may remain there for several years before seeking habitat characteristic of adults of their respective species. Displacement of juvenile mussels by flooding undoubtedly occurs, and passive movements may account for shifts in the distribution of these young cohorts. Ecological and habitat requirements of the juvenile stage remain essentially unknown.

Our estimate of roughly 11,000 juvenile mussels at the study site can be compared with an estimate of adult mussels within a reach of BMC that included our 100 m site. Quadrat sampling of adult mussels in this reach provided an estimate of 50,580 adult mussels in 2700 m^2 of run and riffle habitats (Weaver, 1981). Assuming few adults in the pool habitat, this estimate of abundance suggests that roughly 11,000 adult mussels also occurred within our study site. The entire mussel assemblage in this 100 m section of stream therefore consisted of approximately 22,000 adults and juveniles. *Medionidus conradicus* was the most common species of the adults collected in quadrat samples (Zale and Neves, 1982a), but *Villosa nebulosa* and *V. vanuxemi* were tentatively identified as most abundant among the juveniles collected.

In a previous study of age class structure of the more common species in BMC, Zale (1980) calculated an adult mortality rate of 7 to 19% among ages 4 to 9 years. In the Thames River, Negus (1966) reported annual mortality rates of 5 to 12% for adult *Anodonta anatina* (Linné). It thus appears that mortality declines significantly after mussels reach sexual maturity. The large number of age classes in the mussel populations of BMC (Zale, 1980; Moyer, 1984), and the high mortality of juveniles and their relatively low abundance, all indicate that low but apparently continuous annual recruitment is sufficient to maintain a healthy mussel assemblage in BMC.

To obtain an alternate estimate of adult mussel abundance at the study site for comparison with the quadrat value of 10,715 adults, we used the best available data on population statistics. Previous investigations have calculated annual mortality rates of 5 to 19% for adult mussels (Negus, 1966; Zale, 1980), and maximum ages of the species in BMC between 22 and 56 yrs (Moyer, 1984). To compute a range for the number of mussels at the site, we used our estimate of ages 3 juveniles (2058) as the typical cohort size; used two mean annual mortality rates (10 and 15%) for cohorts of age 4 and older; and assumed a somewhat conservative maximum age of 22 yrs for all species. The number of individuals in each computed cohort (all species combined) was summed between ages 4 and 22 to provide a theoretical estimate of adult mussels at the site. Our estimate was 16,019 mussels, based on an adult mortality rate of 10%, and 11,132 mussels based on 15% annual mortality. The estimate of adults based on a mortality rate of 15% compares favorably with the initial estimate from previous quantitative sampling. Although several assumptions were made in using these population data and treating all species together, we believe that the admittedly rough estimates of mussel abundance for juveniles and adults provide a realistic assessment of the mussel assemblage at this site.

Our success in locating juvenile mussels in BMC is attributed to the reproductive success of apparently healthy populations and the meticulous procedure for processing samples to locate specimens. The juvenile stage is by no means abundant, and the contagious distribution of these early cohorts necessitates numerous samples, even in known habitat, to document their occurrence at specific locations in streams. Although the lack of juveniles (poor recruitment) in other studies has been attributed to sedimentation, pollution, or eutrophication (James, 1985), many of these previous failures to locate juveniles in streams and rivers can probably be attributed to insufficent or inefficient sampling.

The correlation between the abundance of juvenile mussels and that of fingernail clams, and the numerous habitats occupied by the invading Asiatic clam (*Corbicula fluminea*) in BMC and other streams are cause for concern. Although spatial competition between this exotic clam and adult freshwater mussels was postulated (Fuller and Imlay, 1976; Kraemer, 1979), we believe that the juvenile stage of mussels is probably most susceptible to competitive interactions for space or food with this species. The mode and efficiency of reproduction weigh heavily in favor of the Asiatic clam, and declines in mussel populations may go unrecognized for several years because of the difficulty in collecting younger cohorts. It appears therefore that documenting the presence of juvenile mussels in a mussel assemblage may be the only sure way of assessing the relative viability of those populations.

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STRUCTURE OF FRESHWATER SNAIL COMMUNITIES: SPECIES-AREA RELATIONSHIPS AND INCIDENCE CATEGORIES

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ABSTRACT

Freshwater snails in ponds and lakes of two geographic subregions of the northeastern United States were analyzed for species-area relationships and incidence categories. Species diversity in southern New England was positively correlated with area, calcium, and dissolved inorganic carbon, and negatively correlated with sodium/calcium ratio. Diversity in eastern New York State was positively correlated with area, pH, dissolved inorganic carbon, and conductivity. New York diversity was negatively correlated with sodium and altitude. Data from both regions were combined to define incidence categories for common species. Freshwater snails fit criteria for modified incidence categories: high-S species, A-B tramps, C-D tramps, and supertramps.

The number of species on a habitat island has been viewed as an equilibrium between immigration and extinction rates (MacArthur and Wilson, 1967), with some islands having a stable biotic core (Diamond and May, 1981). The relationship between area and species number has been investigated for a number of different organisms (reviewed in Connor and McCoy, 1979), including freshwater mollusks (Sepkoski and Rex, 1974; Lassen, 1975; Aho, 1978a, 1978b, 1978c; Browne, 1981). The relationship is usually expressed by the power function:

$$S = CA^Z$$

or its $\log_{10}$ conversion:

$$\log S = \log C + Z \log A.$$

Number of species = S; Area = A. C is a constant (= y-intercept) representing, in theory, the equilibrium number of species for 1 unit of area (see Gould, 1979). The exponent Z is the slope of regression line and denotes how rapidly the species number increases with increase in area. Connor and McCoy (1979) review the historic use of this and other models. The biological significance of Z has been debated (Connor and McCoy, 1979; Sugihara, 1981; Connor *et al.*, 1983), but its value as a descriptive and comparative tool is unquestioned.

Diamond (1975) expanded the theory of island biogeography to examine not only species number but types of species within each community. He analyzed bird species of the Bismarck Archipelago by "incidence categories". Incidence functions (J) describe the percent occurrence of a species on a group of islands with a particular species number (S). If a species occurs on 30% of the islands having two species, the J value for an S of 2 would be 0.30. Graphing J values against S illustrates a species' distribution pattern in regard to communities of various diversities. Diamond (1975) established six incidence categories: high-S species, A-, B-, C-, and D-tramps, and supertramps.

Freshwater gastropod communities from two regions of northeastern United States are examined using the island biogeographic models of MacArthur and Wilson (1976) and Diamond (1975). Species-area relationships and effects of environmental variables on diversity will be examined and compared to northern European data of Lassen (1975) and Aho (1978a,b,c) for Denmark and Finland, respectively. Incidence categories of common snail species will be described and life history traits compared to those theorized by Diamond (1975) as fitting each incidence category.

DESCRIPTION OF STUDY AREAS

Region I (Fig. 1) encompasses part of southern New England (Connecticut and part of eastern Massachusetts). This region is Atlantic Coastal, with relatively flat to low ridge topography. The lakes tend to have relatively soft waters

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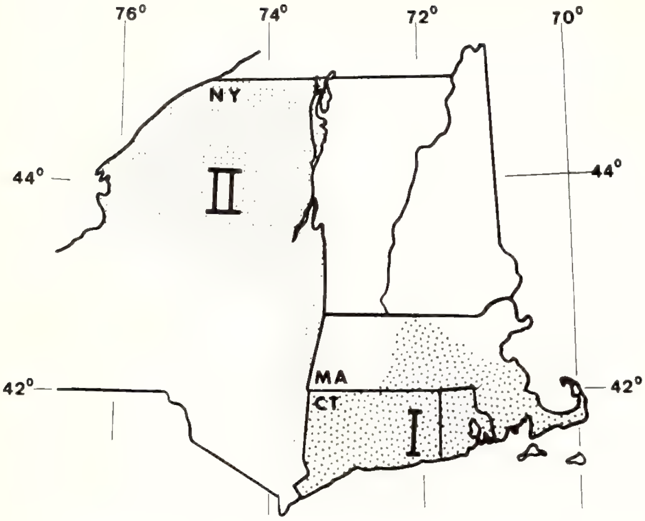

Fig. 1. Geographic areas of ponds and lakes sampled for snails. Region I consists of all of Connecticut (CT) and part of eastern Massachusetts (MA). Region II covers part of eastern New York State (NY), including the Adirondack Mountains.

(down to 1 ppm Ca^{++}) except for regional hard-water areas such as the Taconic Valley of western Connecticut. Many lakes and ponds are impoundments. Lakes close to the Atlantic coast are also subject to sea spray and may have higher amounts of sodium than calcium. Details on Connecticut lakes are described elsewhere (Jokinen, 1983). Ranges in environmental variables for Region I are: pH: 5.1 - 10.0; Ca^{++} : 0.6 - 35 ppm; Mg^{++} : 0.1 - 16 ppm; Na^{+} 1.8 - 40 ppm; K^{+} : 0 - 8 ppm; dissolved inorganic carbon (DIC): 0.3 - 33 mg C/*l*; Na^{+}/Ca^{++} ratios: 0.1 - 12; conductivity: 33 - 346 μmhos/cm; altitude : 1.5 - 360 m.

Region II (Fig. 1) encompasses northeastern New York State and includes the St. Lawrence-Champlain lowlands, northeastern part of the Erie-Ontario lowlands, northern part of Hudson-Mohawk lowlands, and the soft water, acid lakes of the Adirondack Mountains. A summary of the main geologic features of New York is given by the New York State Museum and Science Service (1966). Ranges of environmental variables are: pH: 5.2 - 8.3; Ca^{++} : 1 - 74 ppm; Mg^{++} : 1 - 24 ppm; Na^{+} : 1 - 193 ppm; K^{+} : 0 - 9 ppm; DIC: 1 - 36 mg C/*l*; conductivity: 23 - 1755 μmhos/cm; Na^{+}/Ca^{++} ratio: 0.1 - 8; altitude: 29 - 600 m.

The study area was divided into two regions because of observed molluscan species differences between the Hudson River-Lake Champlain systems and the Connecticut River-Housatonic River systems in western New England (Smith, 1982; Jokinen, unpublished data). Mountains between the two regions appear to have acted as barriers to west-east molluscan dispersal (Smith, 1982).

MATERIALS AND METHODS

Data were collected from New England from 1975-1983 and from New York during 1984. Smaller lakes and ponds generally were visited once while larger lakes, such as Champlain, were sampled five to six times. Most collecting was done by a visual search of vegetation, shorelines below and just above the water lines, submerged rocks, and organic debris. Netting was used where vegetation was heavy, and digging was used to find burrowing species.

Snails were anaesthetized for 8 hours in sodium nembutol (van der Schalie, 1953), tricaine methanesulfonate, or propylene phenoxytol, and preserved in 70% ethanol.

Water samples were taken at each site and reflect midsummer daylight values. The following methods were used for analyses: pH - Corning Model 10 pH meter and combination electrode; dissolved inorganic carbon (as mg carbon/liter) - MSA Model 202 Infrared Carbon Analyzer; conductivity (μmhos/cm) - YSI Model 31 Conductivity Bridge, cell constant = 0.1; cations (calcium, magnesium, sodium, potassium) - by atomic absorption and emission with a Perkin Elmer Atomic Absorption Spectrophotometer Model 306.

Data were analysed using the SAS (Statistical Analysis System) (SAS Institute, 1982) on The University of Connecticut's IBM 3081 computer. Species-Area regressions were analyzed with two models: a) the linear log conversion of the power model:

$$\log S = \log C + Z \log A$$

and; b) a non-linear (quadratic), least squares, iterative model:

$$\log S = \log C + Z \log A + B (\log A)^2.$$

The B term is a parameter fit whose sign (negative or positive) defines the concavity or convexity of the curve. The linear model allows comparison between this and other studies. The non-linear model more clearly fits the data (see May, 1975) and accounts for changes in slope going from small ponds to larger lakes.

Regression analysis was used to examine the relationships of various environmental variables to one another. Forward stepwise linear regression with maximum r^2 technique (SAS Institute, 1982) was used to determine the influence of non-area environmental factors on species diversity. Standard errors for incidence functions were calculated by the formula (see Arkin and Colton, 1970):

$$\text{S.E. of a proportion} = pq/n.$$

RESULTS

CORRELATIONS BETWEEN ENVIRONMENTAL VARIABLES

Correlation coefficients (r) of environmental factors for lakes larger than 10 ha are given in Tables 1 and 2. Smaller lakes and Lake Champlain (113,030 ha) were deleted from the analyses to remove effects of extremes in area. New England lakes (Table 1) had significant positive correlations between species number (S) and calcium and DIC. Calcium was also positively correlated with pH, DIC, conductivity, altitude, and area. The larger lakes of Connecticut are found in the western

Table 1. Correlations (r) between environmental variables of Region I (New England) lakes greater than 10 ha, N = 46. S = species number, DIC = dissolved inorganic carbon as mg C/l, Cond = conductivity in μmhos/cm, Alti = altitude in meters, A = lake area in hectares. Significance: * = $.01 \leq p \leq .05$; ** = $.001 \leq p \leq .01$; *** = $.0001 \leq p \leq .001$.

	S	Ca	Na	Na/Ca	pH	DIC	Cond	Alti
S	—							
Ca	.3387*	—						
Na	-.2861	.0647	—					
Na/Ca	-.4778**	-.4150**	.2824	—				
pH	.2870	.7140***	.1449	-.2435	—			
DIC	.3147*	.9250***	-.0838	-.3829*	.6122***	—		
Cond	.1306	.8433***	-.3523*	-.1741	.7137***	.6716***		—
Alti	.1166	.4538**	-.0237	-.4010*	.3818*	.4770**	.2888	—
Area	.2443	.2982*	-.1940	-.1648	.1196	.4342**	.0045	.3529*

marble valleys. The pH values were correlated with DIC, conductivity, and altitude. DIC was positively correlated with conductivity, altitude, area, calcium, and pH. Significant negative correlations existed between sodium/calcium ratios and S, calcium, DIC, and altitude. Results indicate that higher altitude lakes (e.g., those farther from the coast and out of the extremely soft water regions) have higher calcium, pH, and DIC. High altitude lakes also show a drop in sodium/calcium ratios. The positive correlations between calcium, conductivity, DIC, and pH are to be expected.

New York lakes had similar results except for the effects of altitude. Diversity, calcium, pH, DIC, sodium, and conductivity values decreased with higher altitudes, reflecting the soft water, acidic lakes of the Adirondack Mountains. Whereas altitude was not significantly correlated with S in New England, it was negatively correlated with diversity in New York. This again reflects the low diversity of the Adirondack Lakes.

Tables 3 and 4 summarize best fit models (untransformed data) for the dependent variable, diversity (S), against eight independent environmental variables (pH, calcium, sodium, area, DIC, and sodium/calcium ratio, altitude, and conductivity). New England (Table 3) variables affecting diversity were area (positive correlation) and sodium/calcium ratios (negative correlation). New York (Table 4) variables were area (positive correlation) and altitude (negative correlation).

SPECIES-AREA RELATIONSHIP

Figures 2-4 illustrate the species-area curves for log-log transformed data. Lakes with periodic drawdown and/or no snails were deleted from the statistical analyses. The slopes (Z) of the linear equations of the two regions were 0.1557 ± 0.0245 (F = 40.52, r = 0.5798, $p > F = 0.0001$) for New England (Fig. 2) and 0.0776 ± 0.0309 (F = 6.32, r = 0.3654, $p > F = 0.0160$) for New York (Fig. 4). A comparison of figure 2 with figure 4 indicates that the higher slope for New England lakes is due to fewer low diversity lakes over 10 ha. The y-intercepts (theoretically representing the equilibrium number of species in 1 ha ponds) for both regions were similar (New England = 0.6113 ± 0.0346, antilog = 4.08 species for 1 ha ponds; New York = 0.6261 ± 0.0616, antilog = 4.23 species). Both regions show some curvilinearity in their logS-logA relationships (solid lines on Figs.2-4). Figures 2 and 4 show a concave curvilinearity which indicates an increase in slope (rate of species increase with area) as lakes increase in size. This rate change is more marked for New England (Fig. 2) than for New York.

Lakes of sodium/calcium ratios greater than 2 were deleted from a second series of New England regressions (Fig. 3) because of the negative correlation of diversity with high sodium/calcium ratios. The slope of the linear regression (0.1535 ± 0.0174) remained about the same as that for all New England lakes (Fig. 2). The y-intercept, however, increased to 0.6814 ± 0.0250 (antilog = 4.80 species for 1

Table 2. Correlations (r) between environmental variables of Region II (New York) lakes greater than 10 ha (excluding L. Champlain), N = 29. S = species number, DIC = dissolved inorganic carbon as mg C/l, Cond = conductivity in μmhos/cm, Alti = altitude in meters, A = lake area in hectares.

	S	Ca	Na	Na/Ca	pH	DIC	Cond	Alti
S	—							
Ca	.4570*	—						
Na	-.5351**	.2946	—					
Na/Ca	.1664	-.3195	.6693***	—				
pH	.3936*	.5439**	.2821	-.2592	—			
DIC	.4140*	.8674***	.2163	-.3305	.4342*	—		
Cond	.4245*	.8678***	.5126**	-.0819	.5088*	.7575***	—	
Alti	-.6122***	-.5886**	-.3549*	.1233	-.5859*	-.4519*	-.5322*	—
Area	-.0945	-.1547	-.0926	.0506	-.1514	-.0973	-.1493	.1272

Table 3. Best fit model of New England (Region I) freshwater snail diversity against eight independent variables (area, calcium, pH, and Na/Ca ratio, sodium, dissolved inorganic carbon (DIC), altitude, and conductivity) as determined by forward stepwise regression (maximum r^2 improvement technique). Only lake area and Na/Ca ratio are significant; $r^2 = 0.2950$.

	DF	SS	MS	F	p>F
Regression	8	184.31	23.04	2.20	0.0472
Error	42	440.43	10.49		
Total	50	624.75			
	B-value	**SE**	**Type II SS**	**F**	**p>F**
Intercept	3.1928				
Area	0.0340	0.0126	76.02	7.25	0.0101
Na/Ca ratio	-0.7744	0.3194	61.64	5.88	0.0197
Calcium	-0.4784	0.2895	28.63	2.73	0.1059
DIC	0.2713	0.2096	17.58	1.68	0.2024
Conductivity	0.0193	0.0160	15.36	1.46	0.2330
pH	0.6624	0.8616	6.20	0.59	0.4463
Altitude	-0.0013	0.0018	5.24	0.50	0.4837
Sodium	-0.0290	0.1083	0.75	0.07	0.7906

Table 4. Best fit model of New York (Region II) freshwater snail diversity against eight independent variables (area, calcium, pH, sodium, sodium/calcium ratio, dissolved inorganic carbon (DIC), altitude and conductivity) as determined by forward stepwise regression (maximum r^2 improvement technique). Only lake area and altitude are significant; $r^2 = 0.6828$.

	DF	SS	MS	F	p>F
Regression	8	613.60	76.70	9.15	0.0001
Error	34	285.05	8.38		
Total	42	898.65			
	B-value	**SE**	**Type II SS**	**F**	**p>F**
Intercept	5.0848				
Area	0.0002	0.0000	322.06	38.41	0.0001
Altitude	-0.0030	0.0010	70.75	8.44	0.0064
Na/Ca ratio	1.7486	1.2365	16.77	2.00	0.1664
Calcium	0.1129	0.0821	15.88	1.89	0.1778
DIC	-0.1078	0.1151	7.35	0.88	0.3557
Conductivity	-0.0057	0.0120	1.87	0.22	0.6396
pH	0.4380	1.0098	1.58	0.19	0.6672
Sodium	-0.0143	0.0999	0.17	0.02	0.8870

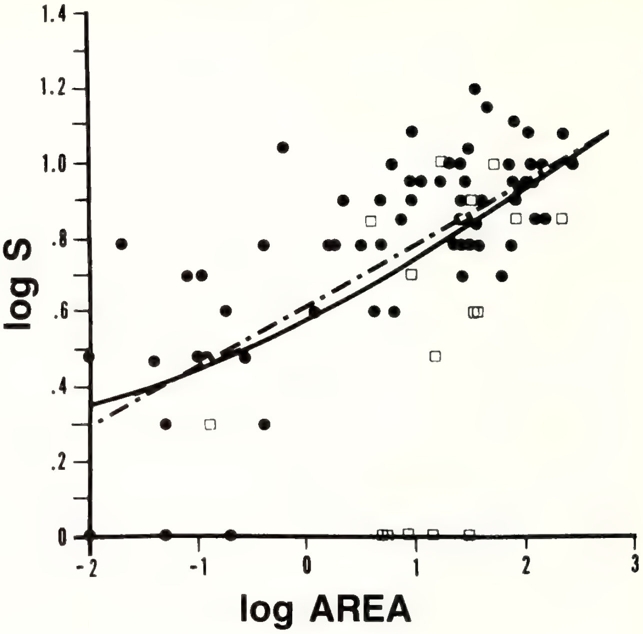

Fig. 2. $\log_{10}$Species - $\log_{10}$Area curves for snails in southern New England lakes and ponds (Region I). Area is in hectares, N = 82 ponds and lakes. The solid line ($\log S = 0.5982 + 0.1495 \log A + 0.0092 (\log A)^2$) was determined by non-linear, least squares iteration. The dashed line ($\log S = 0.6113 + 0.1557 \log A$) represents the linear model, r = 0.5798***. Open squares are sites with Na/Ca > 2 (see Fig. 3).

ha ponds), and r increased from 0.5798*** for all lakes to 0.7458*** for low sodium/calcium lakes. The curvilinearity also changed when high sodium/calcium lakes were deleted. The nonlinear curve became convex with a decreasing rate of species increase with area increase. The low diversity of some of the midsize lakes (1 - 35 ha) caused by their high sodium/calcium ratios tended to pull the curve downward for that region. Both curves have similar values for lakes over 35 ha.

To better analyze effects of calcium concentration on diversity, regressions were calculated for both regions (not illustrated, see Table 5) for lakes with Ca^{++} values larger than and smaller than 5 ppm (high sodium/calcium lakes omitted). New England low calcium lakes and ponds had a lower y-intercept (0.6010 ± 0.389, antilog = 3.99 species for a 1 ha pond) than high calcium lakes (0.7467 ± .0304, antilog = 5.58 species), but they had a higher slope (0.1885 ± .0258) and a better r (0.8469***). New England high calcium, small ponds tend to have a higher diversity than low calcium ponds of the same size. New York low calcium lakes demonstrated a very different relationship with a zero regression of logS-log A. New York lakes with Ca^{++} greater than 5 ppm showed a significant positive logS-logA with a y-intercept of 0.6093 ± .0646 (antilog = 4.07 species) (similar to low Ca^{++} lakes of New England) and a slope of 0.1055 ± .0341.

INCIDENCE CATEGORIES

Incidence functions were calculated from combined Region I and Region II data for twenty-three species of snails (Figs. 5-7) common enough for statistical analysis. Snails could be placed into the following incidence categories (see Table 6): High-S species (Figs. 5A-E) were always absent from habitats of less than 5 species; A-B tramps (Figs. 5F-H, 6A) were always absent from habitats of less than 3 species; C-D tramps (Figs. 6B-H, 7A-E) were ubiquitous with increasing incidence in high diversity habitats; and supertramps (Figs. 7F-G) were ubiquitous but with decreasing incidence in high diversity habitats.

HABITATS WITHOUT SNAILS

Gastropods were absent from eight of the New

England and five of the New York ponds and lakes. Four of these habitats were temporary ponds of low conductivity (24 - 65 μmhos/cm), DIC (0-0.12 mg C/*l*), and calcium (0.3 - 2.1 ppm). One of the New England lakes was a heavily coppered city reservoir, and one was an acid bog (pH = 5.2, Ca^{++} = 0.9 ppm). Four Adirondack lakes also lacked snails, probably due to low pH (5.2-6.0), low calcium (1-2 ppm), and low conductivity (23 - 28 μmhos) combined with the isolation effects of high altitude. A fifth New York lake had a higher pH (6.7) and calcium (8 ppm) but had a very high sodium with a sodium/calcium ratio of 4.4. Lower pH limits for snail existence differed between New York and New England. In New York, the lower pH limit was 5.8 but in New England it was 5.1, a value similar to Norwegian lakes (Økland, 1983).

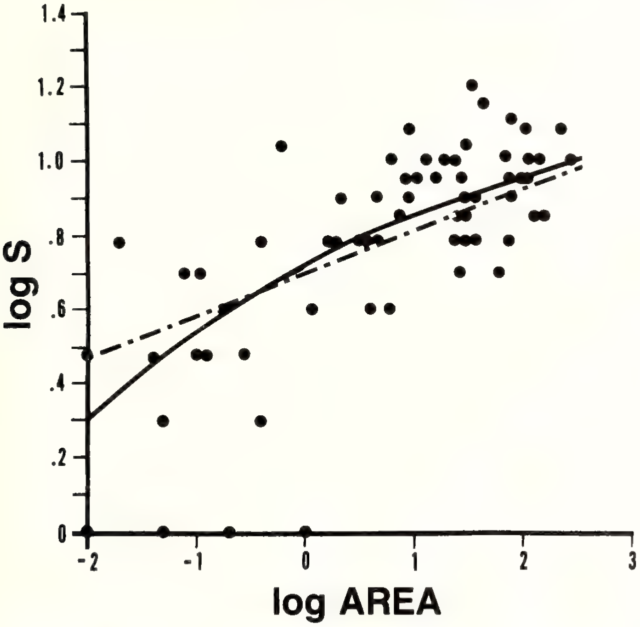

Fig. 3. Log_{10}Species - log_{10}Area curves for snails in New England lakes and ponds (Region I) with Na/Ca ratios < 2. Area is in hectares, N = 65 ponds and lakes. The solid line ($\log S = 0.7208 + 0.1691 \log A - 0.0252 (\log A)^2$) was determined by non-linear, least squares iteration. The dashed line ($\log S = 0.6814 + 0.1535 \log A$) represents the linear model, r = 0.7458***.

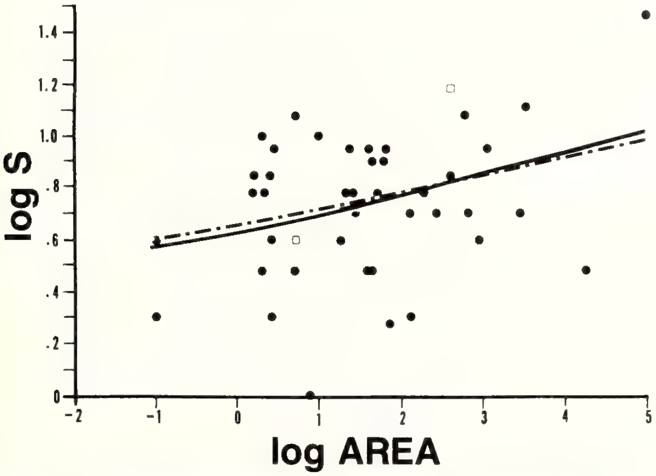

Fig. 4. Log_{10}Species - log_{10}Area curves for snails in eastern New York (Region II) lakes and ponds. Area is in hectares, N = 43 ponds and lakes. The solid line ($\log S = 0.6379 + 0.0519 \log A + 0.0070 (\log A)^2$) was determined by non-linear, least squares iteration. The dashed line ($\log S = 0.6261 + 0.0776 \log A$) represents the linear model, r = 0.3654*. Open squares are sites with Na/Ca > 2.

DISCUSSION AND CONCLUSIONS

SPECIES-AREA

Slopes for the logS-logA relationships of island faunas usually range between 0.17 and 0.35, values theoretically indicating lognormal distributions of organisms (Preston, 1962; MacArthur and Wilson, 1967). These values, however, can just reflect characteristics of regression systems with high r values (Connor and McCoy, 1979). Given this interpretation, slopes between 0.20 and 0.40 may be viewed as the "null hypothesized range" (Connor and McCoy, 1979) and only deviations from this range be viewed as biologically significant.

The slopes for all the calculated lake complexes of this study were less than 0.20. Lakes approaching Z = 0.20 were the New England soft water lakes with high sodium/calcium lakes omitted (slope = 0.1885). The New York lakes (all) had the lowest significant slope (0.0776 ± 0.0309; F = 6.32, r = 0.3656, p>F = 0.0160). New England lakes (all) and New England hard water lakes had intermediate values. The low slope of the New York lakes probably reflects the isolation of the Adirondack lakes (with their depauperate fauna) (Schoener, 1976; Connor and McCoy, 1979) as compared to the "normal" fauna of the harder water lowland ponds. The nonsignificant regression slope of zero (-0.0167 ± 0.0425) for New York lakes of less than 5 ppm Ca^{++} indicates that the larger lakes do not accrue additional species with increased area, and chemical parameters (low pH and calcium) are influencing diversity by increasing extinction rates. A similar situation occurs for the oligotrophic (= soft water) Finnish lakes of the Suomenselka watershed (Aho, 1978a, 1978c). Larger eutrophic (= hard water) lakes of Denmark (Lassen, 1975) and large lakes of the Finnish Lake District (Aho, 1978a) also demonstrated very low slopes (0.09 and 0.061, respectively).

The slope for New England lakes (high sodium/calcium lakes deleted) was similar to the slopes for the subset of smaller lakes and the total number of lakes, overall, of the Finnish Lake District (Aho, 1978a). The highest slope for northeastern United States was calculated for soft water New England lakes. This can reflect a depression of species in soft water small ponds relative to larger lakes. Soft water ponds tend to be high in allochthonous organic matter (fallen terrestrial leaf litter, especially oak) from which tannins leach. Oak filled temporary ponds of New England are very depauperate in species as compared to the hard water, maple filled ponds of the Midwestern United States (Jokinen, 1978, 1983).

Table 5. Linear regression correlations of low (< 5 ppm) and high (> 5 ppm) Ca^{++}). Lakes with sodium/calcium ratios greater than 2 have been omitted.

Region	N	Calcium	slope (Z)	intercept	r	p>F
I	41	>5 ppm	0.1163 ± 0.0217	0.7467 ± 0.0304	0.6510	0.0001
I	23	<5 ppm	0.1885 ± 0.0258	0.6010 ± 0.0389	0.8469	0.0001
II	35	>5 ppm	0.1055 ± 0.0341	0.6093 ± 0.0646	0.4747	0.0040
II	14	<5 ppm	-0.0167 ± 0.0425	0.6627 ± 0.0947	0.1127	0.7011

The similarity of y-intercepts for the New England and New York lake groups probably reflects a similar size in species pool for small (1 ha) to moderate lakes (similar number of "tramp" species). The higher y-intercept of the New England hard water lakes reflects the addition of species restricted to harder waters, e.g., *Valvata tricarinata,* (Say) *Stagnicola elodes* (Say), *Helisoma trivolvis* (Say), (see Jokinen 1983).

The negative correlation of altitude with diversity in New York and lack of correlation of these variables in New England emphasizes the need for initially analyzing distinct geographic areas as separate entities. Mountainous regions may demonstrate different phenomena in diversity patterns from flatlands.

INCIDENCE CATEGORIES

High-S Species. Five snail species can be defined as High-S species and are confined to species-rich islands. Three are prosobranchs [*Valvata tricarinata, Lyogyrus pupoidea* (Gould), and *L. granum* (Say)] and two are pulmonates [*Gyraulus deflectus* (Say), and *Laevapex fuscus* (C. B. Adams)]. *V. tricarinata* appears to need calcium values greater than 10 ppm (Jokinen, 1983; McKillop, 1985), prefers deeper water (Pace *et al.,* 1979), and can require submerged vegetation for egg deposition (Heard, 1963). These requirements make the species relatively uncommon in New England and the Adirondacks. The two species of *Lyogyrus* are very tolerant of low calcium levels but are never found in small ponds. They have an annual life cycle (Jokinen, unpublished data), but little else is known about their natural history. The pulmonate planorbid, *G. deflectus,* can have two reproductive cycles per summer (Jokinen, 1985) or a continuous reproduction from July to October (Gillespie, 1969). *G. deflectus* can be found in ponds over 1 ha and in a wide range of chemical variables (Jokinen, 1983), although it tends to be dwarfed in softer waters (McKillop and Harrison, 1972). The pulmonate ancylid, *L. fuscus*, has a wide range of chemical tolerances and prefers ponds larger than 10 ha. It is protandric (Russell-Hunter and McMahon, 1976) and demonstrates a wide flexibility in life cycle patterns depending upon temperature and food availability (McMahon, 1976).

Diamond (1975) theorized high-S species can represent the extreme of K-selection, have low colonization rates, good competitive abililty, a tolerance for low resource levels, and use overexploitation strategies to reduce resources to a point where their own populations are maintained at a low level and weaker competitors cannot survive. They have the advantage on large islands (with high S) but, because overexploitation tends to reduce population sizes, this group's strategy is not viable on small islands. The High-S snail species probably have low colonization rates due to either high calcium requirements, inability to withstand desiccation on overland travel ("ducks' feet"), or possible requirements for high population densities. They tend not to be the ultimate in K-selected such as are viviparids with their large bodies and relatively small, iteroparitively produced broods. Too little is known about food demands to generalize about resource level demands, and this remains an area open for study.

Table 6. Incidence categories for freshwater snails from Regions I and II (see Figs. 5 - 7).

Family	Species	Incidence Category
Viviparidae	*Cipangopaludina chinensis (Gray)*	C-D tramp
	Viviparus georgianus (Lea)	A-B tramp
	Campeloma decisum (Say)	A-B tramp
Valvatidae	*Valvata tricarinata* (Say)	High-S
Hydrobiidae	*Amnicola limosa* (Say)	C-D tramp
	Lyogyrus pupoidea (Gould)	High-S
	Lyogyrus granum (Say)	High-S
Lymnaeidae	*Stagnicola elodes* (Say)	C-D tramp
	Pseudosuccinea columella (Say)	Supertramp
Physidae	*Physa heterostropha* (Say)	C-D tramp
	Physa ancillaria (Say)	A-B tramp
Planorbidae	*Helisoma anceps* (Menke)	C-D tramp
	Helisoma campanulatum (Say)	A-B tramp
	Helisoma trivolvis (Say)	C-D tramp
	Gyraulus parvus (Say)	C-D tramp
	Gyraulus circumstriatus (Tryon)	C-D tramp
	Gyraulus deflectus (Say)	High-S
	Planorbula armigera (Say)	C-D tramp
	Promenetus exacuous (Say)	C-D tramp
	Micromenetus dilatatus (Gould)	C-D tramp
Ancylidae	*Laevapex fuscus* (C.B. Adams)	High-S
	Ferrissia parallela (Haldeman)	C-D tramp
	Ferrissia fragilis (Tryon)	Supertramp?

A-B Tramps. Tramp species are defined as being present on most species-rich islands but less on increasingly species-poor islands (A- to D-tramps). The species pool for freshwater gastropods is too small to differentiate the four tramp categories of Diamond (1975), so only two categories are defined: A-B tramps and C-D tramps. The A-B tramps are absent from ponds with fewer than three species. Two viviparid prosobranchs, *[Viviparus georgianus* (Lea), and

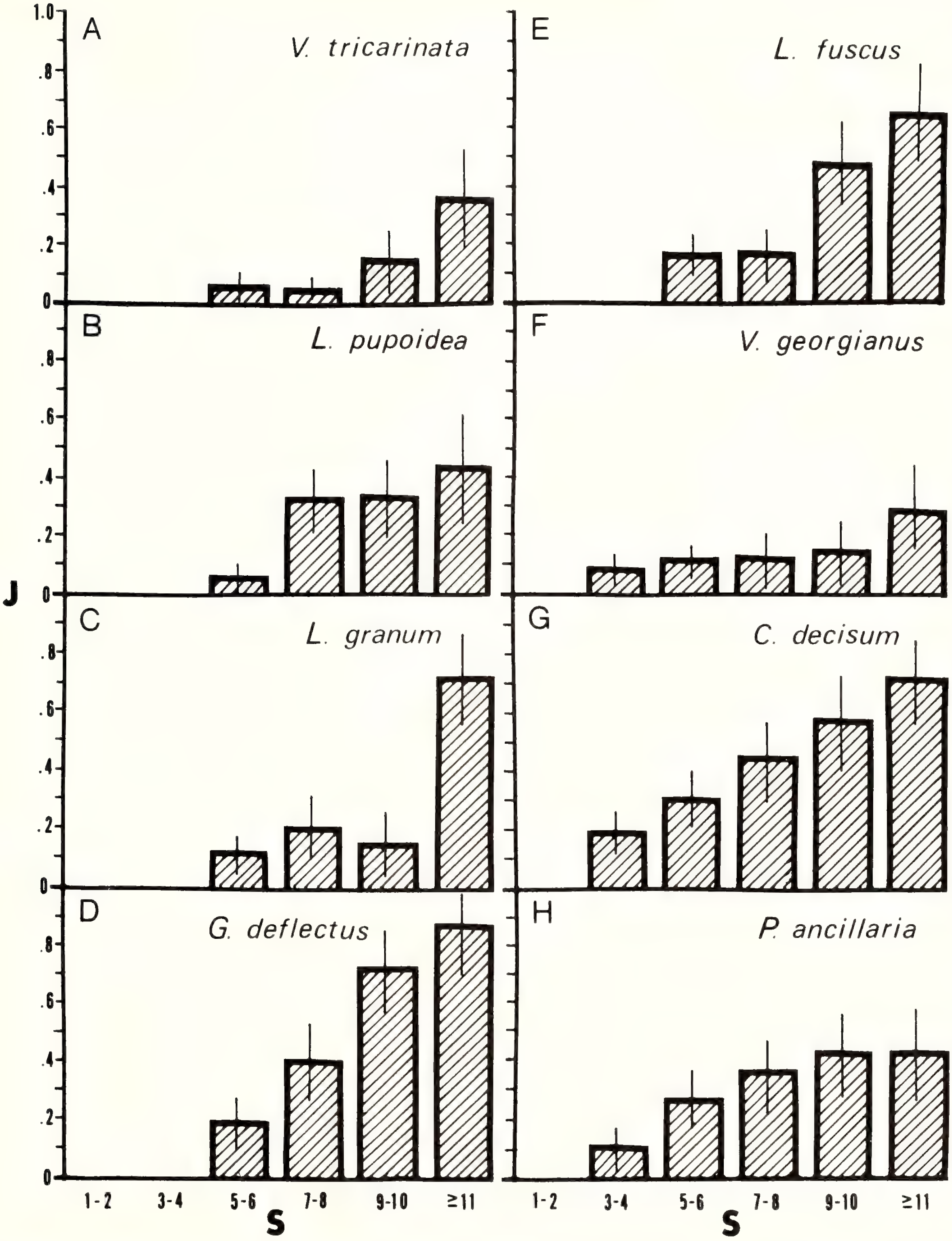

Fig. 5. Incidence functions, J (± 1 S.E.). A. *Valvata tricarinata* (Valvatidae), a high-S species. B. *Lyogyrus pupoidea* (Hydrobiidae), a high-S species. C. *Lyogyrus granum* (Hydrobiidae), a high-S species. D. *Gyraulus deflectus* (Planorbidae), a high-S species. E. *Laevapex fuscus* (Ancylidae), a high-S species. F. *Viviparus georgianus* (Viviparidae), an A-B tramp. G. *Campeloma decisum* (Viviparidae), an A-B tramp. H. *Physa ancillaria* (Physidae), an A-B tramp. N = 167 ponds and lakes for all figures.

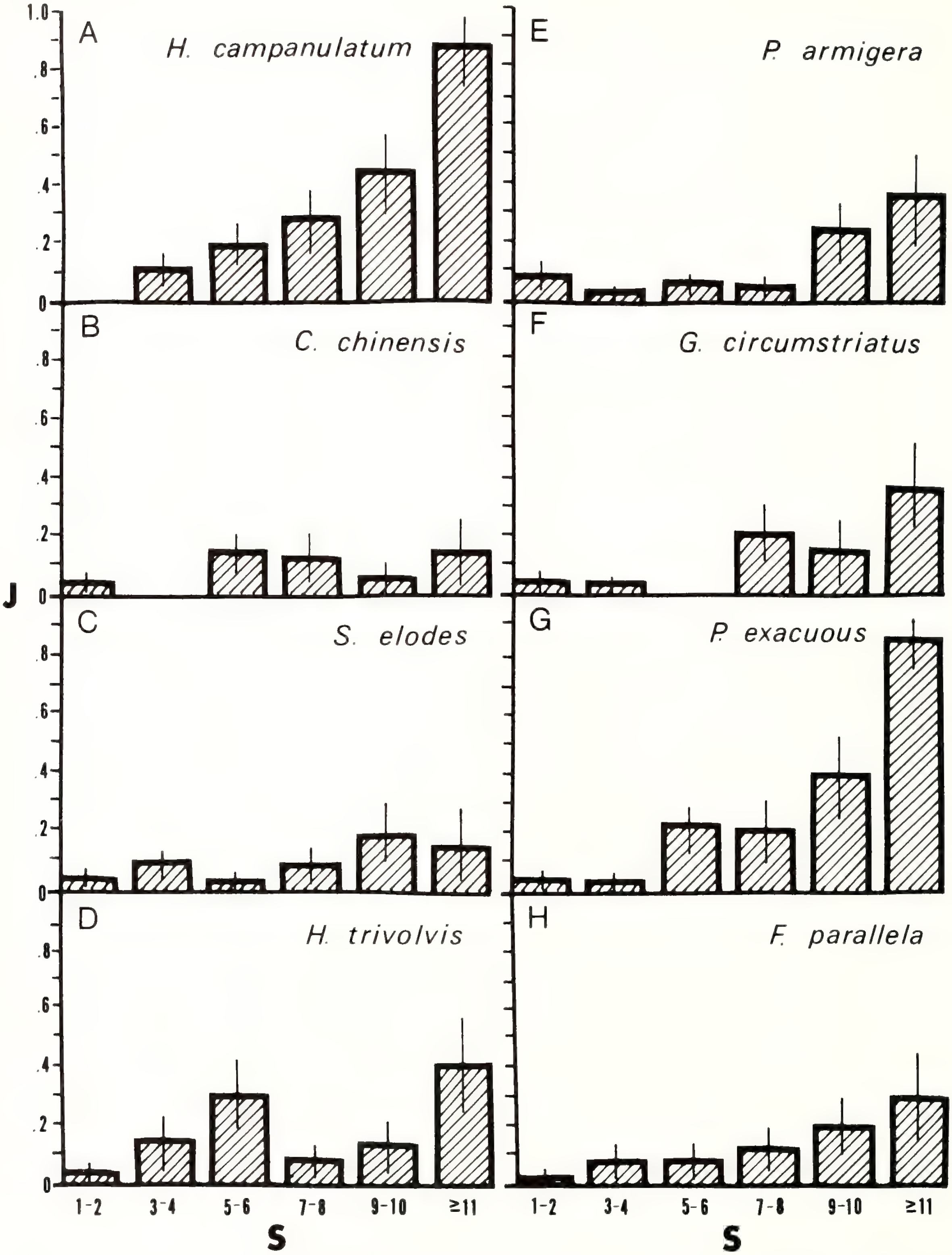

Fig. 6. Incidence functions (± 1 S.E.). A. *Helisoma campanulatum* (Planorbidae), an A-B tramp. B. *Cipangopaludina chinensis* (Viviparidae), an introduced C-D tramp. C. *Stagnicola elodes* (Lymnaeidae), a C-D tramp. D. *Helisoma trivolvis* (Planorbidae), a C-D tramp. E. *Planorbula armigera* (Planorbidae), a C-D tramp. F. *Gyraulus circumstriatus* (Planorbidae), a C-D tramp. (Planorbidae), a C-D tramp. G. *Promenetus exacuous* (Planorbidae), a C-D tramp. H. *Ferrissia parallela* (Ancylidae), a C-D tramp. N = 167 ponds and lakes for all figures.

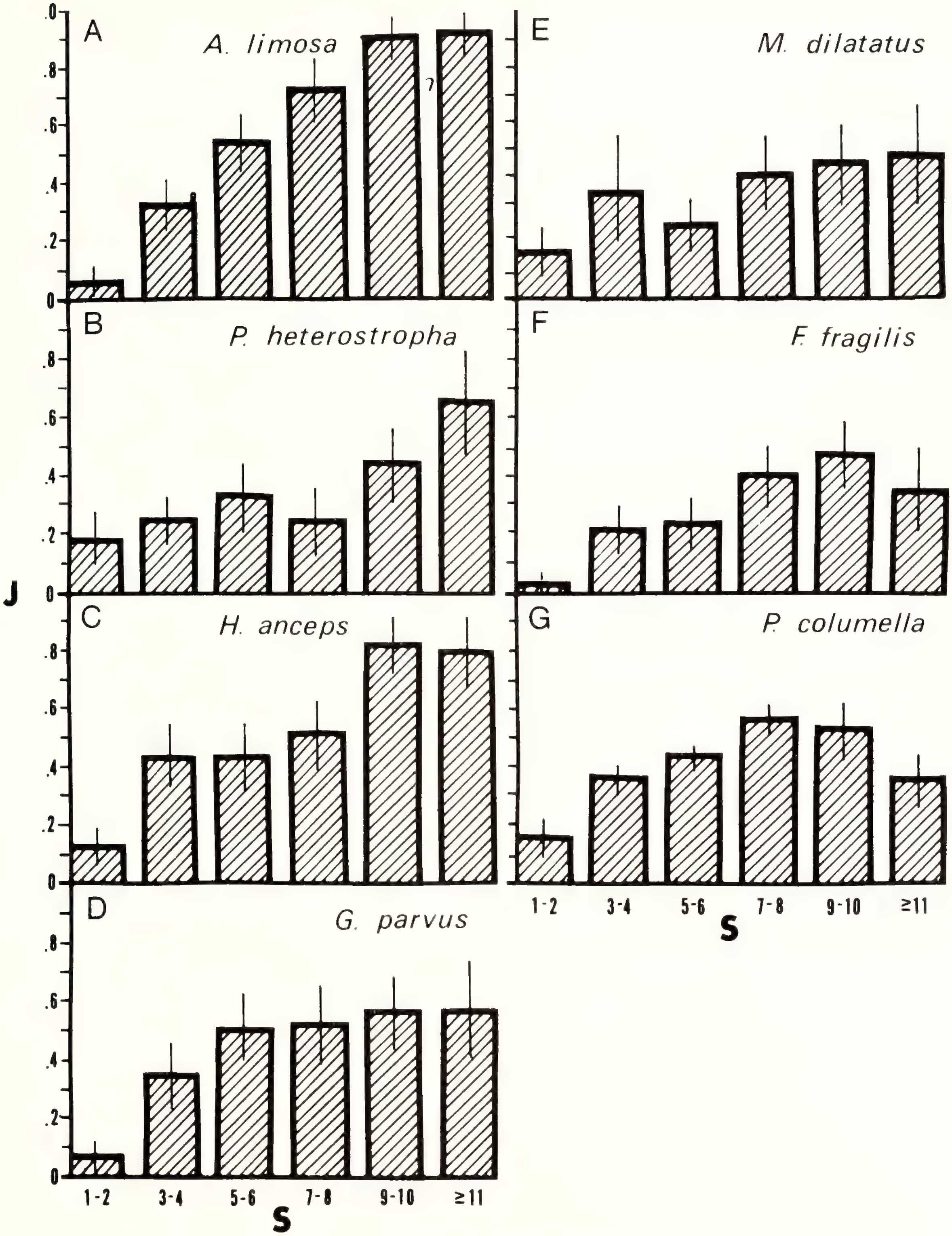

Fig. 7. Incidence functions (± 1 S.E.). A. *Amnicola limosa* (Hydrobiidae), a C-D tramp. B. *Physa heterostropha* (Physidae), a C-D tramp. C. *Helisoma anceps* (Planorbidae), a C-D tramp. D. *Gyraulus parvus* (Planorbidae), a C-D tramp. E. *Micromenetus dilatatus* (Planorbidae), a C-D tramp. F. *Ferrissia fragilis* (Ancylidae), C-D tramp or possible supertramp. G. *Pseudosuccinea columella* (Lymnaeidae), a supertramp. N = 167 ponds and lakes for all figures.

Campeloma decisum (Say)], and two pulmonates [*Helisoma campanulatum* (Say) and *Physa ancillaria* (Say)] are A-B tramps. The two viviparids are long-lived and brood their young (Medcof, 1940; Chamberlain, 1958; Browne, 1978; Jokinen *et al.*, 1982). Northern populations of *C. decisum* are parthenogenetic (van der Schalie, 1965) and are able to survive hypoxic conditions in sand or under logs near shore (Jokinen, unpublished data). *V. georgianus*, a species which has spread into the northeast within the last century (Clench and Fuller, 1965), tends to build up very high population densities (Browne, 1978; Jokinen *et al.,* 1982; Pace and Szuch, 1985). *H. campanulatum* and *P. ancillaria* are annual breeders (Jokinen, 1985) and tend not to be found in small ponds (Jokinen, 1983). All four species are relatively large in size which may limit their dispersal abilities. As a relatively recent arrival, *V. georgianus*, may not have had time to establish its "normal" distribution pattern.

C-D Tramps. C-D tramps are defined as nonendemic species characteristic of habitats occurring on virtually every island. They have longer breeding seasons and more broods/year than other species and are good colonists with the highest tramp dispersal rates (Diamond, 1975). Most of the snails fit into this category. Both prosobranchs and pulmonates are represented. Some of them, such as *Stagnicola elodes*, have the ability to aestivate in dry temporary ponds (Jokinen, 1978; Brown, 1985). Some, such as *S. elodes, Cipangopaludina chinensis* (Gray), and *Helisoma trivolvis*, may be limited to medium and hard water (> 5 ppm Ca^{++}) habitats (Jokinen, 1982, 1983). Other species, such as *Amnicola limosa* (Say), are extremely tolerant of soft water (Jokinen, 1983; Rooke and Mackie, 1984; Servos *et al.*, 1985). With the exception of *C. chinensis* and *H. trivolvis*, all the species are small in size, a facilitation to dispersal. *C. chinensis*, an introduced species, has successfully spread over the northeast (reviewed in Jokinen, 1982). This indicates good dispersal ability (partially anthropogenic) and/or a good ability to colonize a variety of habitats.

Supertramps. Supertramps are confined to species-poor islands. They have the highest dispersal rates, are the best colonizers, are unspecialized in habitat preference, are prone to competitive exclusion, and represent the extreme of r-selection. Supertramps can exist on small islands (with high extinction rates) because they recolonize frequently (Diamond, 1975). The lymnaeid, *Pseudosuccinea columella* (Say), incidence pattern is that of a supertramp. The ancylid, *Ferrissia fragilis* (Tryon), has a pattern which may be interpreted as C-D tramp or supertramp. Both species are highly tolerant of low calcium habitats and are two of the commonest inhabitants of small ponds (Jokinen, 1983). *P. columella* appears to have a remarkable ability to disperse and/or successfully colonize when artificially introduced. It is now spreading in New Zealand (Pullan *et al.*, 1972) and South Africa (van Eeden and Brown, 1966). Both species have more than one brood/year (Jokinen, 1985). There is some indication that *P. columella* and *S. elodes* are mutually exclusive, as are *F. fragilis* and *F. parallela* (Haldeman) (a C-D tramp) (Jokinen, unpublished data). McKillop and Harrison (1972) also observed exclusion of *P. columella* from species-rich habitats.

In conclusion, freshwater snails may be placed into modified incidence functions of Diamond (1975). Further analyses and experimental work on trophic demands and competitive exclusion are necessary to fully analyze how well Diamond's criteria fit gastropods. It appears that K and r-selection criteria do not agree with Diamond's characteristics for incidence categories but dispersal abilities may.

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INTERSTITIAL SUSPENSION-FEEDING BY *PISIDIUM* SPP. (PISIDIIDAE: BIVALVIA): A NEW GUILD IN THE LENTIC BENTHOS?[1]

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ABSTRACT

Observations on the morphology, life position, and behavior of *Pisidium casertanum* (Poli) and *P. conventus* Clessin in Lake Pääjärvi, Finland, suggested that they feed by filtration of suspended microorganisms from interstitial water. Concentrations of interstitial bacteria were as high 2 x 10^9 cells x ml^{-1} in littoral muds. Based on laboratory experiments, both species were able to ingest and efficiently absorb interstitial bacteria from dense suspensions. When offered radiolabelled mixtures of sediment and interstitial bacteria, both species preferentially incorporated interstitial bacteria over particle-associated cells.

Interstitial suspension feeding in muds appears to be a plausible feeding mode for very small animals, such as these two species of *Pisidium*, as long as there is a concentrated food source. The small size of these animals may reflect an adaptation to exploit interstitial bacteria. This feeding mechanism is compared with similar feeding habits of other benthic animals.

Bivalves of the Pisidiidae (Corbiculacea) are cosmopolitan, ubiquitous, and typically prominent members of freshwater benthic habitats. Corbiculaceans, commonly known as fingernail and pea clams, are typically small, and *Pisidium* spp. are strikingly so. Of the 17 species of *Pisidium* recorded from Great Britain, 16 attain a maximum size of 7 mm shell length; only *P. amnicum* (Müller) attains a larger size (up to 13 mm) (Ellis, 1978). *P. moitessierianum* Paladilhe, the smallest European species, becomes sexually mature at 1 mm shell length, and reaches a maximum length of only 1.8 mm (Holopainen, 1979). Thus, small *Pisidium* are only marginally larger than the smallest free-living bivalves known, the pristiglomids, a protobranch family found in deep sea muds (Sanders and Allen, 1973).

The larger corbiculaceans, including such genera as *Corbicula* and *Sphaerium* (family Corbiculidae), obtain food by suspension-feeding upon phytoplankton, although certain species may not meet their energy demands by suspension-feeding and may resort to deposit-feeding (Benjamin and Burky, 1978; Mackie and Qadri, 1978; Hornbach *et al.*, 1984). *Corbicula* populations can reduce phytoplankton abundance in rivers (Cohen *et al.*, 1984). In terms of morphology, gut contents, and filtration behavior, corbiculids are typical suspension-feeding bivalves.

Despite the morphological similarities (other than size) of *Pisidium* spp. to other corbiculaceans, and their importance in freshwater benthos, there does not appear to be a good understanding of their food sources or feeding mechanisms. While several *Pisidium* spp. have been maintained and have grown on diets of bacterial suspensions (Rodina, 1948; Monakov, 1972), it is not clear whether *Pisidium* spp. are deposit feeders, using the ciliated foot as an organ of particle collection, or suspension feeders on interstitial or overlying water. Holopainen and Hanski (1979) suggested that interspecific exploitative competition for food can control the spatial distribution of the two dominant bivalves species, *Pisidium casertanum* (Poli) and *P. conventus* Clessin in a southern Finnish lake. Our first attempts to test this hypothesis underscored the need to understand their food and feeding habits (Holopainen and Lopez, 1984).

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Although *Pisidium* spp. are morphologically similar to other corbiculaceans, laboratory measured filtration rates of *Pisidium* spp. appear to be systematically lower than those of *Sphaerium* spp. (e.g. Alimov, 1981; Hinz and Schell, 1972. See Fig. 1 in Holopainen, 1985). In addition, their adopted life position in mud appears to preclude suspension feeding. The life position of several species has been accurately described (Meier-Brook, 1969), and has been confirmed by our observations (Holopainen, 1985). These highly mobile clams lie dorsal surface downwards at the distal end of a long, blind burrow. Position can vary from just below the sediment surface to a depth of several centimeters. Most of the small species of *Pisidium* are strictly infaunal with no direct access to the overlying water. Water is drawn into the mantle cavity through the pedal aperture. Water is pumped out of the burrow, but overlying water is not inhaled. They have one short siphon that does not reach to the sediment surface (Meier-Brook, 1969, Efford and Tsumura, 1973). The possibility of an infaunal suspension-feeding habit for *Pisidium* has been suggested in several studies. Efford and Tsumura (1973) noted that *Pisidium* can "only siphon interstitial water" and Holopainen and Hanski (1979) suggested that they "obtain their food by filtering microbes from the sediment" (see also Bishop and Hewitt, 1976). The water volumes pumped by small *Pisidium* spp. are so low that it is unlikely that appreciable quantities of overlying water are pulled into the sediment. Moreover, the pressure gradient produced by pumping must be extremely low.

Deposit feeding has frequently been invoked for pisidiids (Mitropolskij, 1966, 1970; Benjamin and Burky, 1978; Hornbach *et al.,* 1984; Burky, 1983). Mitropolskij (1966, 1970) suggested that *Pisidium* spp. use the extensible and highly ciliated foot to collect sediment and to create an inhalant current. Very similar behavior has been described for presiphonate juveniles of the tellinids *Macoma balthica* (L.) (Caddy, 1969) and *Abra alba* (Wood) (Aabel, 1983). Jonasson (1972) pointed out that *Pisidium* can be found in a horizontal burrow just above the redox boundary, and suggested that this is an adaptation to feed at a site of enhanced microbial production. Living food organisms in the sediment appear to affect growth and reproduction of the pisidiid *Musculium securis* Müller, which might indicate a deposit-feeding habit (Mackie and Qadri, 1978). Our observations suggest that deposit feeding is probably not an important feeding mode for the *Pisidium* spp. we studied.

Utilization of dissolved organic matter from interstitial water can also be excluded as an important feeding mode for *Pisidium*. Efford and Tsumura (1973) showed that glucose uptake could only account for a small proportion of the metabolic demands of *P. casertanum*. This result is consistent with the general observation that freshwater animals have more limited abilities to use dissolved organics than do marine animals (Jørgensen, 1976). With these things in mind, we have investigated the feeding behavior and possible food sources of *P. casertanum* and *P. conventus*.

MATERIALS AND METHODS

MICROSCOPIC OBSERVATIONS OF GUT CONTENTS

In order to determine whether or not these two species ingest phytoplankton, we examined the gut contents of field collected animals. Animals were collected in July, 1983, from Lake Pääjärvi, Finland, which has been well studied, and the resident species of *Pisidium* have been investigated in detail (Holopainen, 1978). *P. casertanum* was collected from the shallower (2 to 13 m) regions of the lake, and *P. conventus* was collected from the profundal zone (>25 m). Immediately upon retrieval of the core on board, animals were sieved from the sediment and preserved in formalin. For comparison, specimens of *P. amnicum* and *Sphaerium corneum* (L.) were also examined, the former collected from a creek margin entering Lake Pääjärvi and the latter from the littoral zone of the nearby Lake Lovojarvi. Preserved animals were taken to the Lammi Biological Station. Alimentary tracts were examined with blue light epifluorescence microscopy in order to determine whether algae had been ingested, chloroplasts fluorescing bright red. Approximately 10 animals of each species was examined. Additionally, we made observations on gut fullness and made a qualitative microscopic assessment of gut contents and fecal pellets.

OBSERVATIONS OF FEEDING BEHAVIOR

Observations to determine filtration, particle handling, and living position were made on animals in petri dishes and in thin (1 cm width) plexiglass aquaria viewed from side. Small (2 to 7 μm) fluorescent particles (Cammen, 1980a) and powdered charcoal were used as particle tracers (Holopainen, 1985).

An experiment was conducted to determine whether *Pisidium casertanum* is capable of filtering dense suspensions of interstitial bacteria. Sediment was collected from the littoral zone of Lake Pääjärvi, and pore water squeezed through an 11 μm screen in a Swinnex filter holder, then refiltered through a 3 μm nuclepore filter. The resulting suspension was opaque and opalescent due to an extremely high bacterial concentration (approximately 10^9 cells x ml^{-1}). Animals were placed in this suspension for 3 hours.

ABUNDANCE OF INTERSTITIAL BACTERIA IN LAKE PÄÄJÄRVI

Because there is no standard technique for quantifying interstitial bacteria, we compared capillary tubes, centrifugation, and pore water squeezing. In all cases, bacteria were prepared for enumeration by acridine orange staining and filtration onto 0.2 μm nuclepore filters (Hobbie *et al.,* 1977). The first method, based on techniques of Perfielev and Gabe (1969), consisted of pressing a vertically held capillary tube (0.2 or 0.4 mm) into a sediment core so that the lower opening was approximately 1 cm below the sediment surface. Pore water drawn into the tube by capillary action was diluted in 0.2 μm filtered lake water before staining and counting. The second method involved placing top 2 cm of a core into centrifuge tubes and centifuging for 10 minutes at 750 x g. The supernate was decanted and allowed to settle for 15 minutes to remove larger mineral grains. The interstitial suspension prepared in this manner typically constituted approximately 50% of the total sediment volume. In the third method, 5 cc of sediment was placed into a 10 ml syringe, and pore water squeezed through a 3 μm nuclepore filter fitted in a Swinnex filter holder.

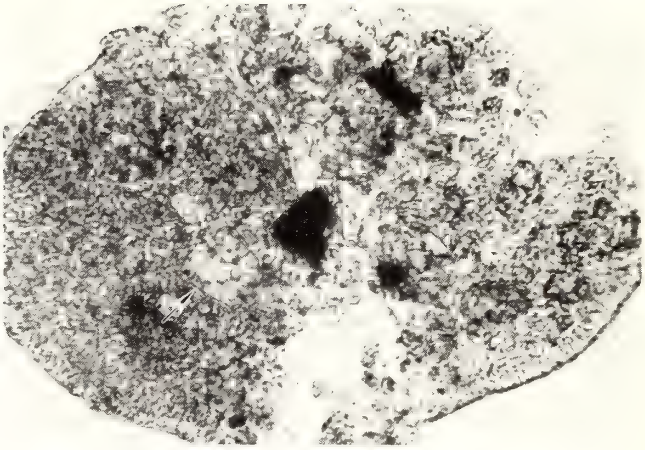
INGESTION AND ABSORPTION OF BACTERIA BY *PISIDIUM CASERTANUM* AND *P. CONVENTUS*

Laboratory experiments were conducted to determine whether or not these two species ingest and absorb interstitial bacteria.

ABSORPTION EFFICIENCY OF INTERSTITIAL BACTERIA

Several experiments were conducted, but because results were similar, only one is described here. An interstitial suspension was prepared by centrifugation (see above) of sediment collected from 18 m depth in Lake Pääjärvi. There were 8.2×10^7 cells x ml^{-1} in the suspension. A 12 ml sample was then labelled for 20 hours with 30 μCi ^{14}C-glucose and 37 μCi ^{51}CrCl$_3$ (see Lopez and Cheng, 1983 for details of radiolabeling methodology). Unincorporated isotopes were removed from the suspension by repeated centrifugations and rinsings with filtered lake water, and then the suspension was brought back to its original volume.

Animals had been collected from Lake Pääjärvi and allowed to acclimate to laboratory temperature (approximately 18° C) for several days. Sixteen specimens of each species were placed in the labelled suspension and allowed to feed for 1 hour. Half of the animals were then sacrificed to determine ^{51}Cr:^{14}C of the ingested material, while the rest were allowed to feed on an unlabelled interstitial suspension for 2 hours. Fecal pellets were then collected and prepared for liquid scintillation counting. Animals and pellets were solubilized in tissue solubilizer (NCS, Amersham). The scintillation cocktail consisted of (9:1) mixture of PCS (Amersham) and 1M HCl. Samples were counted on an LKB liquid scintillation counter using standard two-channel technique with external standards corrections. (Wightman, 1975; Cammen, 1977). Absorption efficiency was estimated by the ^{14}C:^{51}Cr twin-tracer method (Calow and Fletcher, 1972; Cammen, 1980b; Lopez and Cheng, 1983).



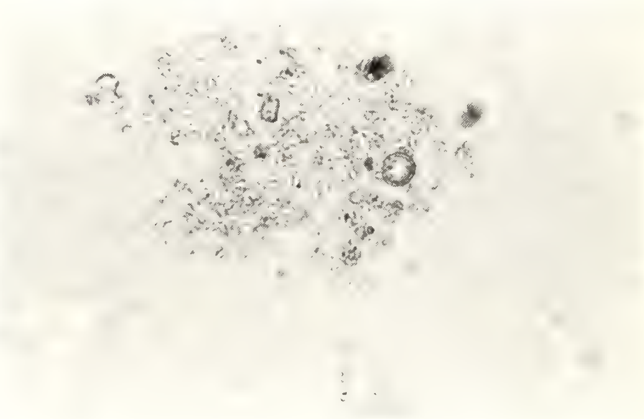


Fig. 1a. Fecal pellet from *Pisidium conventus.* A few mineral grains, some as large as 20 μm (arrow) are visible. The pellet is 175 μm long. **1b.** Extremely loose pellet produced by *Pisidium conventus* consisting almost entirely of small (<5 μm) globular particles. Mineral grains are very rare. The pellet is 110 μm long.

INGESTION/ABSORPTION OF INTERSTITIAL AND SEDIMENT-BOUND BACTERIA

A series of experiments was conducted to determine whether or not *Pisidium casertanum* or *P. conventus* preferentially feed upon interstitial bacteria over particle-bound bacteria . Interstitial suspensions and sediment were separated by centrifugation. Interstitial suspensions and sediment suspensions were then split into two, and 5 ml subsamples of each were labelled either with ^{3}H (thymidine or glucose) or with ^{14}C-glucose. (20 μCi ^{3}H, 10 μCi ^{14}C). After approximately 5 hours of labelling, labelled suspensions were then centrifuge-rinsed to remove unincorporated isotopes, and brought up to original volumes. Then interstitial and sediment suspensions were mixed together in a 1:1 proportion, thereby producing a sediment with approximately natural water content. In treatment I, interstitial bacteria were labelled with ^{3}H and particle-bound bacteria with ^{14}C, while in treatment II, suspensions were labelled in the reciprocal manner. For each treatment, 3 groups of 4 *Pisidium casertanum* or *P. conventus* were placed in 2 ml of mixture in small wells of a multiwell dish. After 2.5 hours, animals were transferred to lake water, allowed to crawl for several minutes to remove much of the adhering sediment, then moved to unlabelled sediment for 1 hour. Animals were then prepared for liquid scintillation counting, first taking care to remove shell encrustations. Isotope incorporation in animal tissue is a measure of the amount of bacteria absorbed from each fraction.

In trial 1, sediment collected from 8 m was labelled with ^{3}H-thymidine and ^{14}C-glucose, and offered to *Pisidium casertanum.* In trial 2, 14 m sediment, labelled as above, was offered to both species. In trial 3, 18 m sediment was labelled with ^{3}H- and ^{14}-C glucose, and offered to both species.

RESULTS

MICROSCOPIC ANALYSIS OF GUT CONTENTS

Many chloroplasts were visible in guts of *Pisidium amnicum* and *Sphaerium corneum*, but none was observed in *P. casertanum* or *P. conventus*. Based on gut contents examination, *P. amnicum* and *S. corneum* appear to feed upon suspended phytoplankton.

Observations of animals fixed immediately upon field collection showed that the large stomach was usually empty, and the relatively short intestine was, at most, only partly filled, and in many cases was nearly empty. Passage of particles through the stomach and midgut must be therefore fairly quick. The length of the digestive tract from mouth to anus is twice the shell length in *Pisidium* and almost 3 times that in *Sphaerium*. Such a difference is due mainly to the length of the coil at the end of the hindgut. Material in the hindgut includes particles ingested but not utilized and undigested remains of food particles, as most digestion and absorption presumably takes place in the stomach and digestive diverticula respectively (Owen, 1974; Morton, 1983).

Intestinal contents in *Pisidium* spp. consisted mainly of extremely small, non-mineral particles and rarely, a few mineral particles (Fig. 1 a,b). There were relatively large particles (5 to 25 μm) in the hindgut of *Sphaerium corneum*, while in *P. amnicum* particles were less than 5 μm (Holopainen, 1985).

FEEDING BEHAVIOR

Observations were made on *P. conventus* (2 mm shell length) in thin "antfarm" aquaria. Animals can burrow quickly, moving over 1 cm (5 body lengths) within 5 minutes. Animals established a feeding position, lying dorsal surface downwards at the distal end of a long, blind burrow (Fig. 2). Water movement in the burrow was traced by observation of small particles suspended in burrow water. Water moved unidirectionally from the blind end of the burrow to the opening at the sediment surface. We did not observe any particle collection by the foot.

Animals were often quiescent. In one case we were able to estimate the pumping rate of a *P. casertanum* 3 mm long that pumped actively for some hours. The velocity of burrow water was approximately .006 cm x sec^{-1}, and the cross-sectional area of the burrow was approximately .03 cm^2, so that pumping rate was estimated at 0.6 ml x hr^{-1}.

Pisidium casertanum is capable of suspension feeding upon very dense suspensions. A dense suspension of interstitial bacteria (2 x 10^9 cells x ml^{-1}) was visibly cleared from suspension by 6 animals within 2 hours. Fecal pellets were observed on the bottom of the vial, indicating that the suspension had been ingested.

Under laboratory conditions, *P. casertanum* and *P. conventus* swallowed sedimentary particles when offered dense slurries, although most material collected by the foot was rejected as pseudofeces. The most active fecal pellet

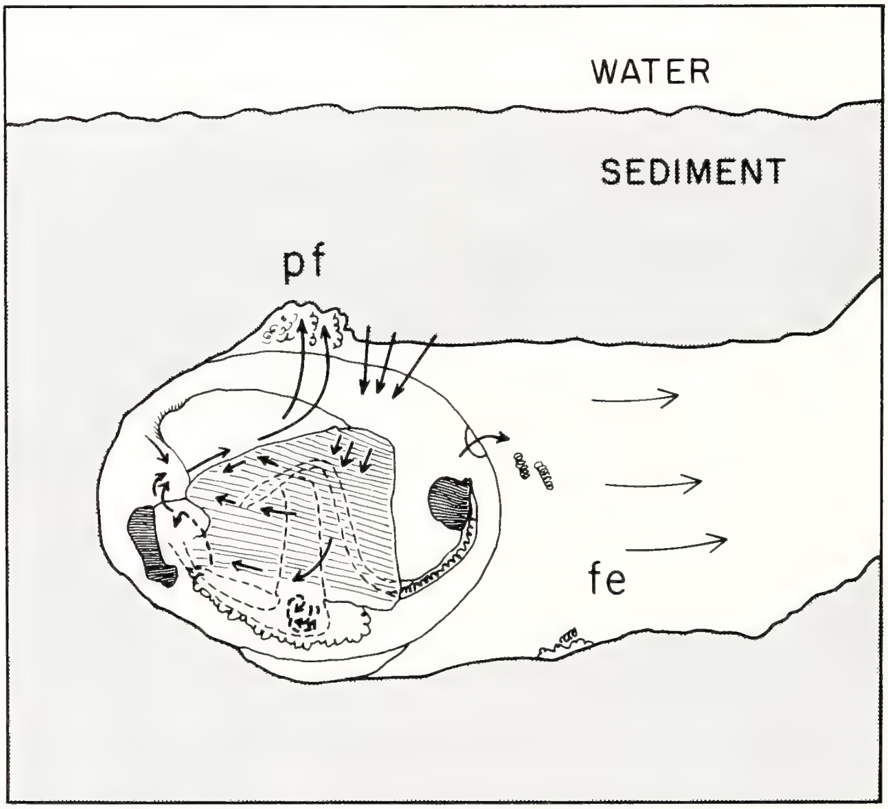


Fig. 2. Typical feeding position of *Pisidium casertanum* and *P. conventus.* Arrows indicate the water currents caused by ciliary action. pf: pseudofeces; fe: feces. This figure is partly adapted from Meier-Brook (1969) and Holopainen (1985).

production rate we observed was 4 pellets per hour, which would be low for a deposit feeder (Cammen, 1980c).

INTERSTITIAL BACTERIA

Bacterial concentrations in the interstitial waters of Lake Pääjärvi sediments proved to be surprisingly high, in the littoral zone averaging 5 x 10^8 cells x ml^{-1} (Fig. 3). The interstitial suspensions consisted mainly of bacteria. The densest suspensions were opaque with bacteria. In contrast, intertidal salt marsh muds, a supposedly more productive habitat than this oligotrophic lake, have interstitial bacterial concentrations ranging from 10^6 (Rublee *et al.*, 1983) to a maximum of 5 x 10^8 cells x ml^{-1} (J. McDonald, pers. comm.). Our preliminary results suggest that centrifugation and capillary sampling give similar results, but samples collected by pore water squeezing are much lower. We did not determine total sedimentary bacterial abundance, but did compare these results with unpublished data obtained from Lake Pääjärvi (I. Bergstrom, pers. comm.). In littoral sediments, approximately 4% of the total bacteria are interstitial, but only 0.5% are interstitial in sediment at 40m.

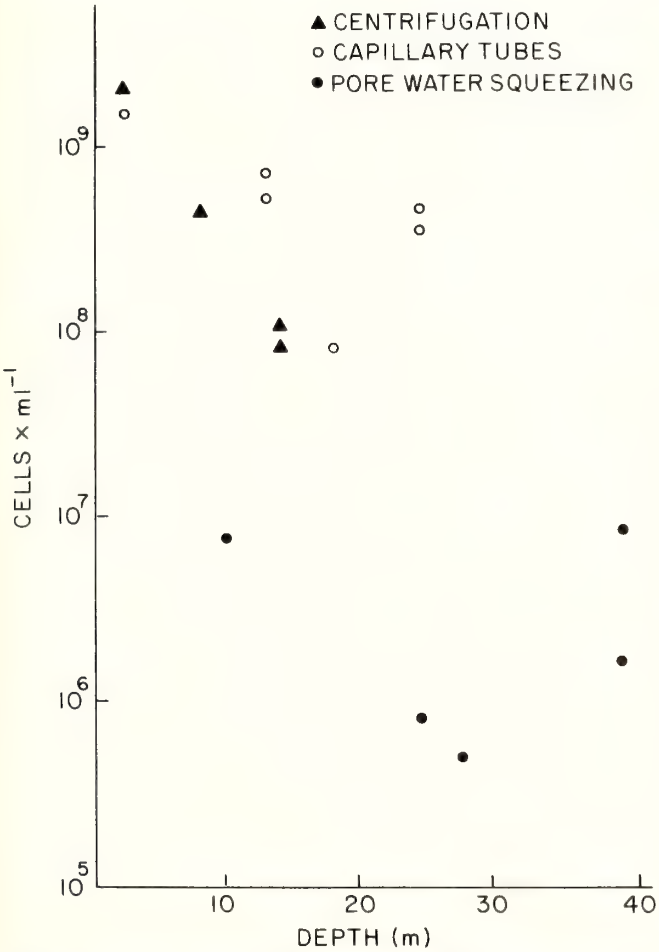


Fig. 3. The relation between abundance of interstitial bacteria and water depth in Lake Pääjärvi. All samples were taken from the top 1 cm of undisturbed sediment cores. Samples collected by pore water squeezing, capillary tubes, and centrifugation are compared.

Although a detailed investigation was not made, our impression was that, at least for the littoral muds, interstitial bacteria were much larger than sediment-associated cells (approximately 1.2 μm^3 vs. 0.2 μm^3).

INGESTION AND ABSORPTION OF INTERSTITIAL BACTERIA

ABSORPTION OF INTERSTITIAL BACTERIA

Both *Pisidium casertanum* and *P. conventus* absorbed approximately half of the ingested bacteria when allowed to feed on a pore water suspension (Fig. 4). Although we were not able to determine clearance efficiency, these two species are obviously capable of filtering natural bacteria from a dense suspension. Bacteria are presumed to be too small for filtration by most suspension-feeding bivalves (Wright *et al.*, 1982).

These estimates were not corrected for ^{51}Cr absorption (Calow and Fletcher, 1972), nor did we determine whether or not the length of time allowed for egestion was sufficient. Nevertheless, this trial demonstrated that both species ingested and absorbed a natural suspension of interstitial bacteria. Other trials, using sediments collected from different depths, gave absorption efficiency estimates ranging from 40% to 60%.

INGESTION AND ABSORPTION OF INTERSTITIAL AND SEDIMENT-BOUND BACTERIA

In all cases where counts were above background, *Pisidium casertanum* exhibited moderate to extreme selective (2 to 10,000X) incorporation from the interstitial bacteria over the particle-bound bacteria (Fig. 5). Except during trial 2, treatment I, isotope incorporation by *P. conventus* was

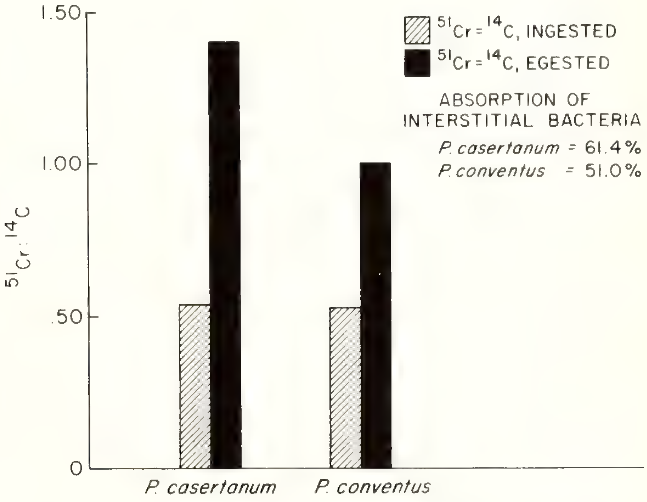


Fig. 4. Absorption of interstitial bacteria by *Pisidium casertanum* and *P. conventus*. Absorption efficiency is calculated as: 100 x (1 - $^{51}Cr:^{14}C$, ingested/$^{51}Cr:^{14}C$, feces) (Lopez and Cheng, 1983).

barely above background, apparently because of their small body size.

DISCUSSION

Experimental results support the idea that *Pisidium casertanum* and *P. conventus* are interstitial suspension feeders, utilizing bacteria and perhaps other small particles suspended in the interstitial water (Efford and Tsumura, 1973; Holopainen and Hanski, 1979). Our observations confirm those of Meier-Brook (1969) that water is being pumped out of the burrow, but not necessarily that overlying water is being pulled into the sediment (Fig. 2). Because it is a blind burrow, the only direct source of nutrient is the surrounding sediment. Similarly, larval lamprey appear to obtain particles suspended in water just above the substratum and also from pore water within sediment (Moore and Mallatt, 1980; Mallatt, 1982). Water is pumped into the sandy sediment, and exhalant water is extruded into the sediment around the burrow. Like ammocoetes, *Pisidium* spp. appear to pump water extremely slowly, and are able to filter very concentrated suspensions of interstitial bacteria. Once filtered, ingested bacteria are absorbed efficiently.

The reciprocal labelling experiments indicate that *Pisidium casertanum* and *P. conventus* preferentially ingest interstitial bacteria from a sediment suspension, but that a substantial fraction of absorbed bacteria came from sediment ingestion. In trials 1 and 2, animals incorporated label more dramatically from ^{3}H-thymidine labelled bacteria than from ^{14}C-glucose labelled cells, indicating an asymmetry in labelling protocol. These results are at variance with gut observations of field collected animals, as mineral particles were rarely observed in the alimentary tract. One of the biggest problems with these experiments is the destruction of sediment texture. Certainly, *Pisidium* spp. ingest sedimentary particles under laboratory conditions, which in this case consisted of rather severe disruption of sediment texture. We suspect that sediment ingestion in these experiments was an artifact of this disruption. Many *Pisidium* species typically live in loose, flocculent sediment with a high water content and a coarse pore structure. In Lake Pääjärvi, water content varied from 60 to 90%, increasing with water depth (I. Bergstrom, unpubl.). Because stomachs and midguts of animals in nature were invariably empty, and gut contents rarely included mineral grains, we doubt whether sediment ingestion is significant under natural conditions. Animals could be induced to feed upon dense sediment suspensions, but at a very low rate of ingestion. We saw no evidence of particle collection by the foot, as described by Mitropolskij (1966, 1970) for *P. casertanum*. Animals were offered a variety of particles, including sediments, fluorescent particles, charcoal powder, and flour. Particles did collect at the pedal gape, this appeared to result from crawling behavior. Sediment particles drawn into the mantle cavity by the inhalent current and are transported to the large labial palps. The palps appear to be efficient in rejecting sedimentary particles.

On first inspection, there appear to be several problems with the postulated interstitial suspension feeding mechanism. One might expect that sediment particles would be drawn in with the inhalant current. More important is the question: Is the density of interstitial bacteria high enough to support such feeding? With regard to the first problem, sediment particles taken into the mantle cavity to be selectively rejected as pseudofeces. Selective rejection of mineral grains has been demonstrated in several species of suspension-feeding bivalves (Kiørboe *et al.*, 1980; Bricelj and Malouf, 1984). The amount of sediment taken into the mantle cavity may depend upon the water velocity caused by pumping, and the texture of the sediment. Because of the small size of most *Pisidium* spp., the absolute pumping rate (ml x hr^{-1}) and the water velocity is very low, even though weight-specific pumping rates may not be particularly low, In aquaria, the measured pumping rate of 0.6 ml x hr^{-1} for *P. casertanum* maintained a water velocity of only .006 cm x sec^{-1} into the burrow.

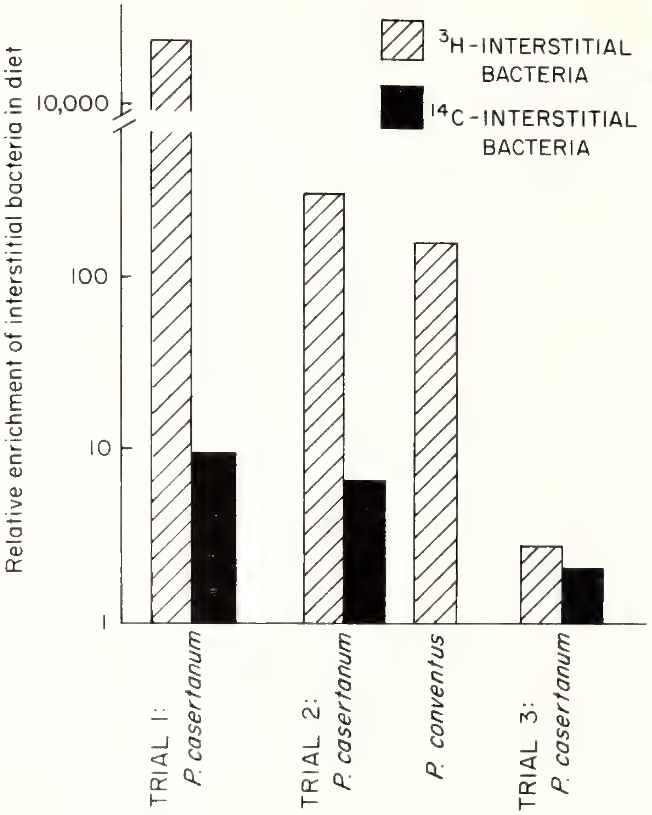


Fig. 5. Ingestion/absorption of interstitial and particle-bound bacteria. Relative enrichment of interstitial bacteria in the diet was calculated as: ^{3}H: ^{14}C incorporated/^{3}H: ^{14}C sediment mixture (where ^{3}H was used to label interstitial bacteria), or ^{14}C:^{3}H incorporated/^{14}C:^{3}H, sediment suspension (^{14}C labelling of interstitial bacteria). Differences among trials is described in the text.

We have used weight-specific respiration rates (Holopainen and Ranta, 1977) and measured interstitial abundance of bacteria to calculate the volume of interstitial water that would have to be filtered to meet metabolic demands. We assume that the carbon content of bacteria is 2 x 10^{-13} g C x cell^{-1} (Tenore, pers. comm.) and that there is 100% clearance and 50% absorption efficiency. The respiration rate of a 0.5 mg (ash-free dry weight) *Pisidium casertanum* is 0.11 μg CO_2 x hr^{-1} at 10°C, and 0.64 μg CO_2 x hr^{-1} at 20°C. If the interstitial concentration of bacteria is 10^7 cells x ml^{-1}, then *P. casertanum* needs to filter 0.03 ml x hr^{-1} to meet respiratory demands at 10°C, and 0.17 ml x hr^{-1} at 20°C. Even if interstitial concentrations is 10^6 cells x ml^{-1}, at 20°C *P. casertanum* still need filter only 1.7 ml x hr^{-1}. Our measured values of interstitial bacteria were typically at least 10^8 in littoral sediments likely to attain temperatures above 10°C. Even at relatively high temperature and low concentrations of interstitial bacteria, therefore, low filtration rates appear to be able to meet respiratory demands.

Given the cosmopolitan distribution of *Pisidium casertanum* and *P. conventus*, it is unlikely that the results presented here are due to some peculiar feature of Lake Pääjärvi. It is a typical mesohumic, oligotrophic boreal lake. There are nine species of *Pisidium* in the lake; *P. casertanum* is the most abundant in the littoral zone, and *P. conventus* is the only species in the profundal zone (> 14 m).

The major morphological difference between pisidiids and corbiculids is the smaller size of most pisidiids. Small size might be the most important morphological adaptation to interstitial suspension feeding. Fenchel (1982) noted that suspension feeders filter 10^4 to 10^5 body volumes daily, so the absolute amount of water filtered by a small animal will be very low. This might be a necessity for animals utilizing pore water, because capillary forces and sediment compaction would constrain water movement. There should therefore be some size limitation to interstitial suspension feeding in muds.

It is difficult to state what the upper size limit to interstitial suspension feeding is in muds, but it is possibly reached even within the pisidiids. In Lake Pääjärvi, the largest pisidiid is *Pisidium amnicum* (up to 13 mm). Its habitat appears restricted to cohesive sediments along stream banks emptying into the lake (Holopainen, unpubl.). Microscopic observations indicated that the intestines of specimens collected in Lake Pääjärvi contained many fluorescing diatoms, very similar to those seen in *Sphaerium* guts. Mineral deposits on the shell suggests that this species is not very mobile. *P. amnicum* is therefore probably maintaining contact with overlying water. In making calculations of volumetric demands for *P. amnicum*, similar to those described above, we noted that at 20°C, a 8.5 mm animal would have to filter 4.1 ml x hr^{-1}. Larger animals would have to filter more.

This atypical suspension feeding on pore water may be controlled by the capillary forces of the interstitial environment. This feeding mechanism should consist of pumping water very slowly, and having the ability to filter very concentrated suspensions (Mallatt, 1982). A concentrated food source may be a prerequisite.

Interstitial suspension feeding by *Pisidium* spp. is reminiscent of feeding behaviors of several other infaunal animals. Another infaunal animal capable of pulling water into a fine-grained substrate is the larval ammocoete of the lamprey *Petromyzon marinus* (L.) (Mallatt, 1982). Suspended food particles are collected from overlying water drawn into the sediment, and also from pore water (Moore and Mallatt, 1980). The marine corbiculid *Polymesoda (Geloina) erosa* (Solander), an infaunal resident of the landward fringe of mangroves, draws in through the siphon overlying water during high tide, but during low tide burrow water is inhaled through the pedal gape (Morton, 1976). Clam burrows lead into networks of crab burrows that always remain filled with water. Presiphonate juveniles of the tellinid bivalve *Macoma balthica* feed by "drawing water and food particles from the interstitial spaces", but this animal ingests large volumes of sediment, so both juvenile and adult *Macoma balthica* are properly classified as deposit feeders (Caddy, 1969). The lucinacean *Fimbria fimbriata* (L.) is a deposit feeder in coral sands, collecting particles via the pedal gape, using the food as the primary particle collector (Morton, 1979). Interstitial suspension feeding, that is filtering particles from pore water, is therefore another class of pedal gape feeding (see Morton, 1983); interstitial suspension feeding and pedal gape feeding are not synonymous, because pedal gape feeders may be filtering burrow water or be deposit feeding.

Perhaps the most interesting comparison is with "an enigmatic case" of the clavagellacean *Brechites penis* (L.), which burrows vertically in stiff muddy sand (Purchon, 1977: 168-170). The anterior end of the shell is closed by a perforated disc, and the muscular anterior pallial partition serves to draw water from the substratum, through the perforated disc. Purchon (1977) suggested that the purpose of this pump is "to embed the shell more deeply in the substratum if it is partly exposed by wave action. It is also possible that fine particles or organic matter may be brought into the mantle cavity as a result of the pumping action and this may be ingested and provide an auxiliary source of food." A more recent morphological investigation on this rare species supports this interpretation (Morton, 1984).

Other small marine bivalves appear to be either deposit feeders (protobranchs and many of the tellinids), or suspension feeders that maintain contact with the overlying water. There are infaunal suspension feeders that do not maintain direct communication with overlying water live in sands and gravels [e.g. the marine bivalve *Astarte castanea* (Say), Stanley, 1970]. We have no good reason to explain this apparent absence of this functional group in marine muds, although it may be related to the abundance of interstitial bacteria. Large marine ciliates bear closer examination in this context.

CONCLUSIONS

There is reasonable evidence that *Pisidium casertanum* and *P. conventus* do not feed by normal suspension feeding, deposit feeding, nor uptake of dissolved organic matter. Our conclusion of interstitial suspension feeding, therefore, is based partly on the negative premise that other obvious feeding mechanisms are lacking. Positive evidence is more tentative (morphology, gut contents, radiotracer experiments) but is consistent with our suggestions that interstitial suspension feeding is the characteristic feeding mode of small species in the genus *Pisidium.* Size can be a constraint of interstitial suspension feeding, and the characteristically small size of many *Pisidium* species can be the result of selection for this feeding mode. The density of interstitial bacteria in the muds of Lake Pääjärvi appeared to be high enough to meet the metabolic demands of small animals. Systematic measurements in marine, estuarine and freshwater muds should be done to determine the factors controlling abundance of interstitial bacteria.

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EFFECTS OF ACIDIFYING ENVIRONMENTS ON FRESHWATER MOLLUSKS IN SOUTHERN ONTARIO, CANADA

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ABSTRACT

Laboratory and field studies on freshwater Mollusca in several low-alkalinity lakes of south-central Ontario indicate that neither the hydrogen ion concentration nor the metal (cadmium, lead, aluminum) concentrations in the lake are lethal as independent or joint toxicity factors. However, changes in the calcareous composition of the shell and changes in shell morphometry can be related to low alkalinity and/or pH of the environment. These changes are accompanied by decreased growth and reproduction that have depressed the production and species diversity of the molluscan communities. As lakes acidify, the epifaunal grazers (gastropods) in the molluscan community are replaced by infaunal filter feeders (Pisidiidae). The mollusks can play an important role in the sources and cycling of carbonates in acidifying environments.

Considerable research has been completed in the last decade on the effects of acidifying environments on freshwater mollusks, especially in Scandinavia (J. Økland, 1969; 1980; Økland and Økland, 1980; K. Økland, 1979, 1980; Økland and Kuiper, 1980) and Canada (Mackie and Flippance, 1983a, b, c; Rooke and Mackie, 1984a, b, c; Servos *et al.,* 1985). These studies have demonstrated direct and indirect effects of low alkalinity environments on mollusks at both the population and community levels (Fig. 1). Although most studies have examined molluscan responses to acidifying environments, evidence indicates that mollusks may alter the response of low-alkalinity lakes to additions of acid precipitation. This paper summarizes the reponses of mollusks in low-alkalinity environments in southern Ontario to additions of acid and the possible effects that mollusks may have on their freshwater milieu.

DIRECT EFFECTS

HYDROGEN ION TOXICITY

High hydrogen ion concentration is lethal to most mollusks. However, each molluscan species has its own median level of tolerance to hydrogen ion concentration (Mackie, 1986). A survey of the literature cited above shows that certain Pisidiidae [e.g. *Pisidium casertanum* (Poli)] are among the last mollusks to disappear from acidifying lakes, suggesting that they should be more tolerant of high hydrogen ion concentration than other freshwater mollusks. Indeed, 96 hr static laboratory bioassays with 10 clams of each species held at 5 pH levels (2.0, 3.0, 4.0, 5.0, 6.0 and a control at pH 7.0) using sulfuric acid (additional methods given in Mackie, 1986), have shown a decreasing order of tolerance in adult *P. casertanum* (LC50 pH = 2.7), *Musculium securis* (Prime) and *Amnicola limosa* (Say) (LC50 pH = 3.0), *Pisidium compressum* Prime (LC50 pH = 3.3), and *Sphaerium striatinum* (Lamarck) and *Valvata tricarinata* (Say) (LC50 pH = 3.5). In the Pisidiidae, the larval stages appear to be more tolerant than the adults to hydrogen ions (Mackie *et al.*, 1983), but in the Hydrobiidae the embryonic stages are much more sensitive than the adults (Servos *et al.*, 1985).

Although excess hydrogen ions are toxic to mollusks, none of the acidifying lakes studied in Ontario, Canada, have hydrogen ion concentrations that exceed the LC50 values found in the laboratory bioassays (Mackie, 1986). This includes the short term pH depressions that occur in the spring in most low-alkalinity lakes (pH = 4.5; Servos, 1983). Therefore, the disappearance of molluscs from acidifying lakes in southern Ontario is not likely due to lethal concentrations of hydrogen ions *per se.* Jewell (1922) concluded that substrate type was a more important variable than pH in determining the distribution of Unionidae in a slightly acidic (pH 5.8 - 7.1) stream in Illinois, and Fuller (1974) and Harman (1974) discuss several variables, including pH and alkalinity, that limit the distribution of mollusks.

Harman (1969) implied that changes in pH in poorly-buffered streams of New York may be at least partially responsible for the eradication of some Unionidae. However, the response of mollusks to acidity may depend on the time of

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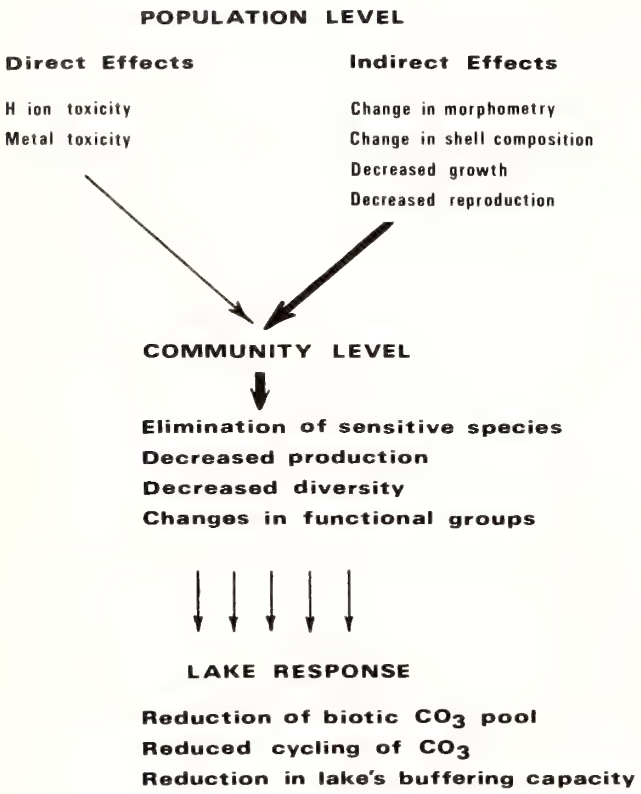

Fig. 1. Summary of direct and indirect effects of acidifying environments on freshwater mollusk communities and the response of low-alkalinity lakes as a result of these effects. Thicker arrows indicate greater effects than thin arrows.

year and/or their level of activity. For example, studies by Servos (1983) showed that many mollusks are inactive or in a dormant state during spring pH depression events, and even if the pH is artificially dropped from 5.5 to 3.5 there is little or no mortality of adult mollusks during these short periods (i.e. hours) of large pH variations. On the other hand, when Matteson (1955) transplanted mussels into lake waters of pH 4.4 - 6.1 for about six weeks during the growing season (June to August), the response of the mussels toward acidity was similar to those toward estivation (i.e. the valves clamp shut, the body-parts decrease in volume, the pH of mantle fluids drop, and all movements cease). Moreover, not all mussels seem to have the same sensitivity or response to low pH; Morrison (1932), Buckley (1977), and Mackie and Flippance (1983c) reported mussels living throughout a broad range (5.50 - 8.63) in pH, with *Elliptio complanata* (Lightfoot, 1786) itself occurring over the entire range.

METAL ION TOXICITY

An increase in hydrogen ion concentration in lakes is usually accompanied by an increase in concentrations of metals, especially cadmium, aluminum, zinc, and lead (Wurtz, 1962; LaZerte, 1984; Moore and Ramamoorthy, 1984). These metals are toxic to mollusks (Wurtz, 1962; Mackie, 1986), and if present in high enough concentrations, will directly eliminate them from contaminated lakes. Mackie (1986) found *Pisidium casertanum* to be more tolerant of Cd, Al, and Pb than *Amnicola limosa* (Table 1). However, the LC50 values for each metal is at least an order of magnitude greater than has been measured in any of the acidifying lakes in Ontario (Mackie, 1986). Moreover, the metals (Al, Cd, and Pb) used in the laboratory bioassays were mainly in the inorganic forms which are more toxic than the organic forms that dominate most low-alkalinity lakes (Borgmann, 1983; LaZerte, 1984). Therefore, it seems unlikely that metal concentrations alone or the joint action of hydrogen ions and metals are lethal to mollusks in the acidifying lakes of southern Ontario, Canada.

Table 1. 96 hr LC50 values (mg l^{-1}) of three metals at pH 4.0 for adults of three species of freshwater mollusks.

SPECIES	Cadmium	Lead	Aluminum
Pisidium casertanum	0.50	16.2	>0.400
Pisidium compressum	0.70	30.8	>0.400
Amnicola limosa	1.20	21.0	>0.400

Other metals, such as copper, mercury, and silver, are also toxic to mollusks (Wurtz, 1962), but their toxicity in acidifying lakes has not yet been investigated. Heavy metal toxicity is affected by hardness and pH (Wurtz, 1962; Arthur and Leonard, 1970) and is a major factor in the disappearance of mollusks below acid-mine drainages and industrial-waste outfalls [Mullican *et al.*, 1960 (*fide* Fuller, 1974); Cairns *et al.*, 1971 (*fide* Harman, 1974); Imlay, 1971; Yokley, 1973]. While the levels of many metals are elevated in acid precipitation (Jeffries and Snyder, 1981; Galloway *et al.*, 1983) and in most acidifying lakes (Schindler *et al.*, 1980; Forstner and Wittmann, 1983; Luoma, 1983), studies on the toxicity of metal mixtures to mollusks, such as those done by Hutchinson and Spraque (1986) on fish, remain to be done.

INDIRECT EFFECTS

POPULATION LEVEL

The most significant effects of acidifying environments on populations of freshwater mollusks are changes in shell composition, shell morphology, reproduction, and growth. There are probably other indirect effects but only these have been reported to date and are elaborated upon below.

The changes in shell composition of mollusks in relation to the buffering capacity of the water have been determined from simple correlations between calcium content of the shell and the alkalinity and pH of the water (Mackie and Flippance, 1983c); Table 2 shows which species exhibit these significant correlations. As might be expected, most species [e.g. *Physella gyrina* (Say), *Cincinnatia cincinnatiensis* (Anthony), *Pisidium casertanum, P. compressum, Sphaerium striatinum, Anodonta grandis* Say, and *E. complanata* (Lightfoot)] show decreasing calcium content of the animal with decreasing alkalinity (i.e. positive correlations). Only one species studied, *Sphaerium rhomboideum* (Say), showed a

Table 2. Summary of significant ($P < 0.05$) correlations between calcium content of freshwater mollusks and pH and alkalinity of the water. Table is based on data given in Mackie and Flippance (1983c). + indicates a positive correlation, – indicates a negative correlation, and o indicates no significant correlation ($P > 0.05$).

GASTROPOD SPECIES	CORRELATION		BIVALVE SPECIES	CORRELATION	
	pH	Alk.		pH	Alk.
Physella gyrina	o	+	*Musculium securis*	o	o
Helisoma anceps	o	o	*Pisidium casertanum*	+	+
Gyraulus parvus	+	o	*Pisidium compressum*	–	+
Amnicola limosa	o	o	*Pisidium variabile*	o	o
Cincinnatia cincinnatiensis	+	+	*Sphaerium rhomboideum*	–	–
Valvata tricarinata	–	o	*Sphaerium simile*	–	o
Campeloma decisum	o	o	*Sphaerium striatinum*	+	+
			Anodonta grandis	+	+
			Elliptio complanata	+	+
			Lampsilis radiata (Gmelin, 1792)	o	o

significant negative correlation indicating that as alkalinity decreases, the calcium content of the animal increases. However, this species is found only in waters with alkalinities greater than about 40 mg $CaCo_3$ l^{-1}. Most species in Table 2 also show a significant positive correlation with pH; those species that show negative correlations are without exception characteristic of high alkalinity environments.

There is also some evidence that certain species of mollusks have greater amounts of carbon in their shells than other species in acidifying lakes (Mackie *et al.*, 1983). Table 3 shows the carbon content of the shell of several species from neutral (near pH 7) lakes. It is interesting to note that the most sensitive species in the list (*Sphaerium striatinum*) has the least amount of carbon and the most tolerant (*Pisidium casertanum*) has the most carbon in the shell.

Among the most interesting effects are the changes that occur in shell morphology, as detected in canonical correlation analyses (Mackie and Flippance, 1983a). The most significant canonical variates ($P < 0.0001$) indicate that a shortening of the shell with an increase in calcium content and total weight is related to decreasing alkalinity and pH in relation to calcium and total hardness for *Valvata tricarinata*, *Campeloma decisum* (Say), *Pisidium casertanum*, and *P. variabile* Prime (Fig. 3). For *Amnicola limosa, Sphaerium simile* (Say), and *S. striatinum*, the shortening of the shell and an increase in calcium content and total weight is related to decreasing alkalinity and calcium hardness relative to total hardness; pH is less important as a variable. Only three species [*Helisoma anceps* (Menke), *M. securis* and *P. compressum*] of fifteen studied showed increasing shell size without changes in shell weight as alkalinity increased in relation to calcium or total hardness. Within the Unionidae, shorter, heavier shells in *Elliptio complanata* are related to increasing alkalinity, total hardness, and pH relative to calcium hardness. In *A. grandis*, shorter, heavier shells are related to decreasing alkalinity relative to total hardness; calcium hardness and pH seem less important.

Table 3. Calcium carbonate and carbon content of shells in common species of freshwater mollusks. The species are arranged in order of decreasing calcium carbonate content. 95% confidence intervals are given in parentheses. N.D. denotes that carbon content was not determined.

SPECIES	Shell CaCO as % of total dry wt.	μg C mg^{-1} shell
Elliptio complanata	93.3 (3.51)	7.68 (2.41)
Sphaerium striatinum	92.2 (1.69)	5.33 (0.68)
Sphaerium simile	90.7 (2.53)	N.D.
Pisidium compressum	90.3 (0.89)	N.D.
Anodonta grandis	90.1 (4.08)	N.D.
Campeloma decisum	89.6 (1.44)	8.24 (2.01)
Amnicola limosa	88.7 (3.00)	6.11 (1.02)
Valvata tricarinata	88.0 (0.92)	N.D.
Helisoma anceps	80.8 (1.75)	N.D.
Physella gyrina	80.6 (2.68)	7.33 (1.33)
Musculium securis	80.0 (3.21)	8.32 (1.57)
Pisidium casertanum	65.8 (1.66)	10.18 (2.77)

The canonical correlation analyses of Mackie and Flippance (1983a) also indicate that acidifying environments have different effects on different species of mollusks. In many species (e.g. *Amnicola limosa, Valvata tricarinata, Campeloma decisum, Pisidium casertanum, P. variabile, Sphaerium simile, S. striatinum, Amnicola grandis,* and *Elliptio complanata*) a high density of calcium carbonate can be maintained in the shell by forming shorter, heavier shells. Hence, the protection offered by the calcareous shell is maintained. The only difference among the species is the factor or set of factors that seem to be related to these changes. For all but *E. complanata* the shorter, heavier shell may be considered a defensive mechanism since it is observed in waters with decreasing alkalinity, pH or calcium hardness. The only species that can afford long, thin shells are those that are characteristically found in high-alkalinity water (e.g. *P. compressum*). Such species appear to have no defensive mechanisms for decreasing alkalinity and are eliminated from

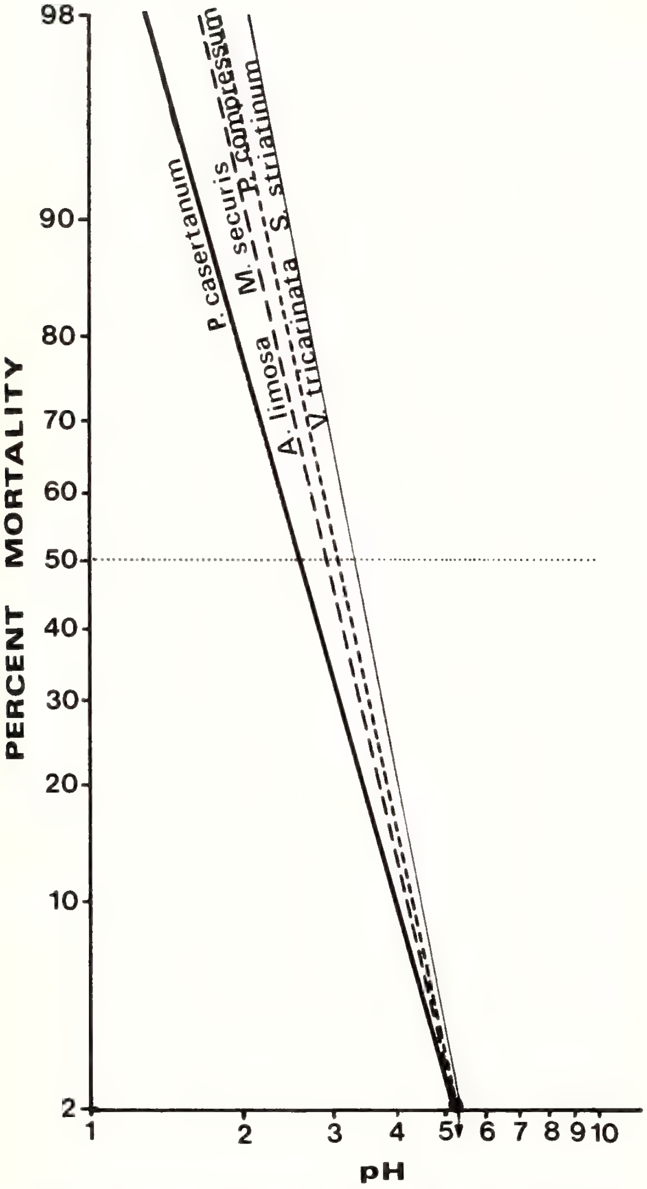

Fig. 2. 96 hr LC50 plots for pH for six species of freshwater mollusks in static laboratory bioassays. Data are from Mackie (1986).

waters with alkalinities less than about 20 mg $CaCo_3$ l^{-1}. *E. complanata* exhibits another type of response where the shell becomes increasingly thinner as acidification proceeds. In fact, some populations in low-alkalinity lakes of southern Ontario have such thin shells that they are difficult to pick up without pushing the fingers through the shell. It is possible that dissolution of calcium carbonate from the shell may be buffering the excess hydrogen ions within the internal milieu of the clam.

Perhaps the most significant effect of decreasing pH and alkalinities is the decreased reproductive capacities of mollusks. Rooke and Mackie (1984c) reported reduced production of eggs and extramarsupial larvae in *Amnicola limosa*

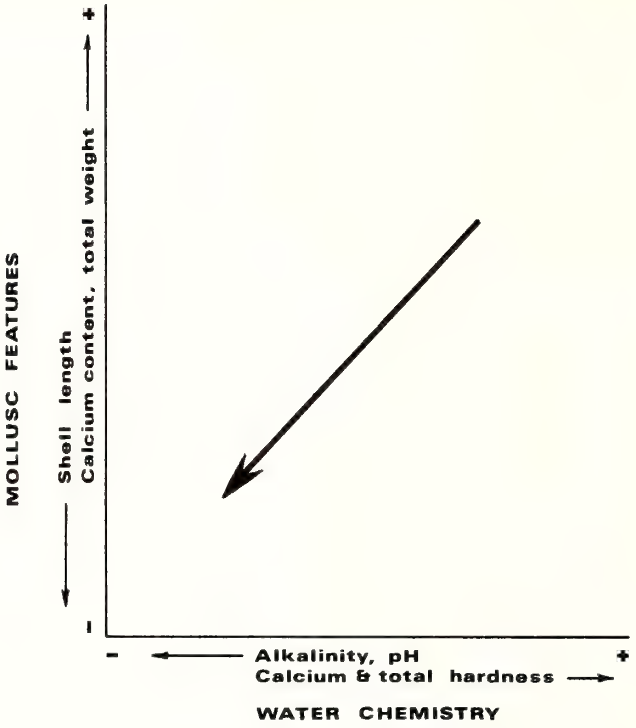

Fig. 3. Summary of the most common significant canonical correlation for the first canonical variate on data reported by Mackie and Flippance (1983a). The graph shows that shell length tended to decrease relative to calcium content and total weight of the species examined (see text) as the pH and alkalinity decreased relative to the calcium and total hardness of the water.

and *Pisidium casertanum* in lakes with total alkalinities below 1 mg $CaCo_3$ l^{-1} (Fig. 4).

An equally significant effect is the impaired development of eggs at low pH. Servos *et al.* (1984) reported impaired development of eggs of *A. limosa* in the laboratory at and below pH 5.0 and delayed development at pH 5.5 relative to pH 6.0 (Fig. 5); they also reported slightly reduced natalities in *Pisidium casertanum* and *P. ferrugineum* Prime in low-alkalinity lakes relative to higher-alkalinity lakes.

There is also good evidence that the growth of some mollusks are affected in low-alkalinity lakes. Rooke and Mackie (1984c) found that the growth rates of *Amnicola limosa* were greatest in high-alkalinity lakes (0.013 mm day^{-1}) and least in low-alkalinity lakes (0.008 mm day^{-1}). However, in the same study Rooke and Mackie were unable to show any effects of low-alkalinity environments on the growth of *Pisidium casertanum* or *P. ferrugineum*.

COMMUNITY LEVEL

The above results clearly indicate that acidic environments are affecting the biology of freshwater mollusk populations. These effects differ for each species of mollusk but ultimately one can expect to observe declines in production and diversity as lakes acidify. This has been observed

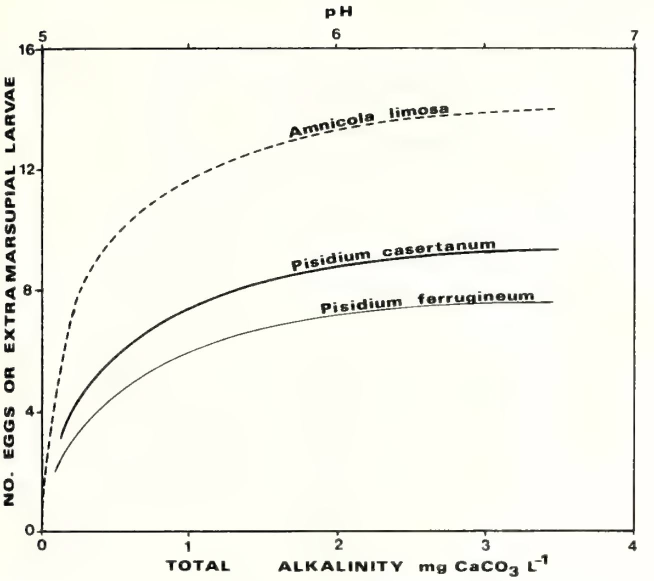

Fig. 4. Trends in natalities of three species of mollusks common in low-alkalinity lakes in south-central Ontario. Curves are based on data reported by Servos *et al.* (1985).

in low-alkalinity lakes of southern Ontario, Canada (Figs. 6, 7). Rooke and Mackie (1984c) reported greater levels of annual production of *Amnicola limosa* in higher alkalinity lakes (70 - 80 mg m^{-2}) than in low-alkalinity lakes (0 - 26 mg m^{-2}). However, the annual production of some species of Pisidiidae (*Pisidium casertanum, P. ferrugineum*) appeared to be similar between low- and high-alkalinity lakes. Nevertheless, the annual production of other pisidiids (including *P. compressum, P. variabile,* and *Sphaerum striatinum*) must be affected because they are not found in low-alkalinity lakes.

Using data in Mackie and Flippance (1983c), figure 7 shows extremely large variations in the numbers of species of freshwater mollusks in lakes with high alkalinities (greater than about 20 mg $CaCo_3$ l^{-1}). Hence, factors other than pH and alkalinity seem to affect the diversity of mollusks in environments with alkalinities exceeding about 20 mg $CaCo_3$ l^{-1}, but below this value, pH and alkalinity explain a large part of the variation in diversity. Harman and Berg (1971), Harrel and Dorris (1968), Harrison *et al.* (1970), and Houp (1970) have all reported direct correlations between alkalinity and production and diversity of mollusks, but all studies were done on waters with alkalinities exceeding 20 mg $CaCO_3$ l^{-1}. Hunter (1964) claims that calcium is a better predictor of species diversity; waters with > 25 mg Ca l^{-1} can support all molluscan species in a geographic region, waters with 10 to 25 mg Ca l^{-1} can support 55%, waters with 5 to 10 mg Ca l^{-1} can support about 40%, and waters with < 3 mg Ca l^{-1} support less than 5%.

Finally, the type of faunal community also seems to be affected. The community appears to change from one containing a large proportion of epifaunal grazers (e.g. gastropods) to infaunal filter feeders (e.g. Pisidiidae). The organisms that survive the longest in low-alkalinity lakes appear to be those that are associated with the sediments, perhaps because the sediments have a greater capacity to buffer additions of hydrogen ions than does the water.

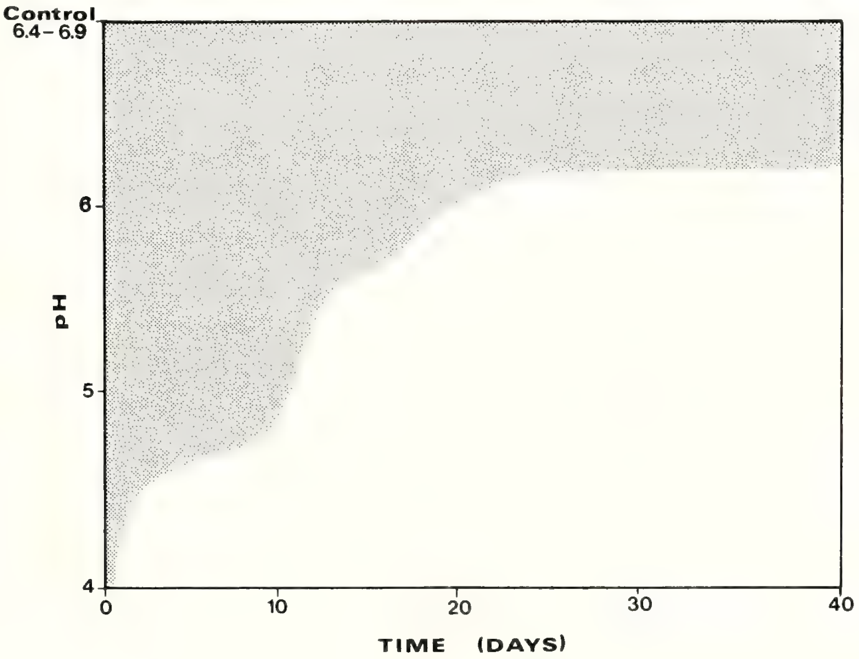

Fig. 5. Graph to show the times at which eggs of *Amnicola limosa* kept at different pH's fail to keep pace with eggs kept at pH 6.4 to 6.9 (i.e. control) (e.g. eggs kept at pH 5 are at the same stage of development as the control eggs for up to 10 days, after which eggs at pH 5 fail to develop). Graph is based on data in Servos *et al.* (1985).

LAKE RESPONSES

Since mollusks contain such large amounts of calcium carbonate in their bodies (namely the shell) one would expect that mollusks can provide a source or carbonate for the buffer systems of acidifying lakes. If molluscan carbonates are formed from carbon dioxide there must be a concomitant release of acid because the negative carbonate ion cannot be formed from neutral carbon dioxide without the liberation of protons. Mollusks should, therefore, produce acid during the process of shell formation, above and beyond that for any heterotrophic organism. Once the mollusks die the synthesized carbonates should be released and contribute to the carbonate pool of the environment. Hence, mollusks can play a role in the sources, cycling, and storage of carbonates. These conclusions are supported by the studies of Rooke and Mackie (1984b) who used a series of aquaria containing various combinations of water, sediment, and mollusks to investigate the effects of mollusks on the alkalinity of the water. They found that live mollusks acidified the water and dead, decomposing mollusks were associated with an increase in alkalinity. Aquaria containing dead mollusks had more stable alkalinity concentrations than aquaria with burrowers, or aquaria with just sediments and water when all received additions of ''acid rain'' (pH 4.1). Non-molluscan invertebrates liberated acid-neutralizing materials from the sediments but the source was quickly depleted. These general trends are depicted in figure 8.

Similar experiments were also performed in the field under more natural conditions, using a trough system (Mackie *et al.*, 1983). The trough was divided into three channels; one was treated with limestone, one was treated with unionid

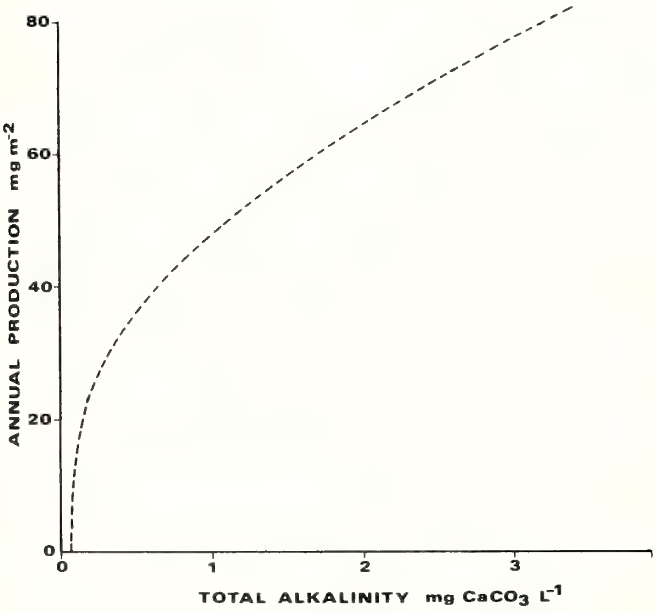

Fig. 6. Annual production of *Amnicola limosa* in relation to total alkalinity of the environment. Based on data in Rooke and Mackie (1984c).

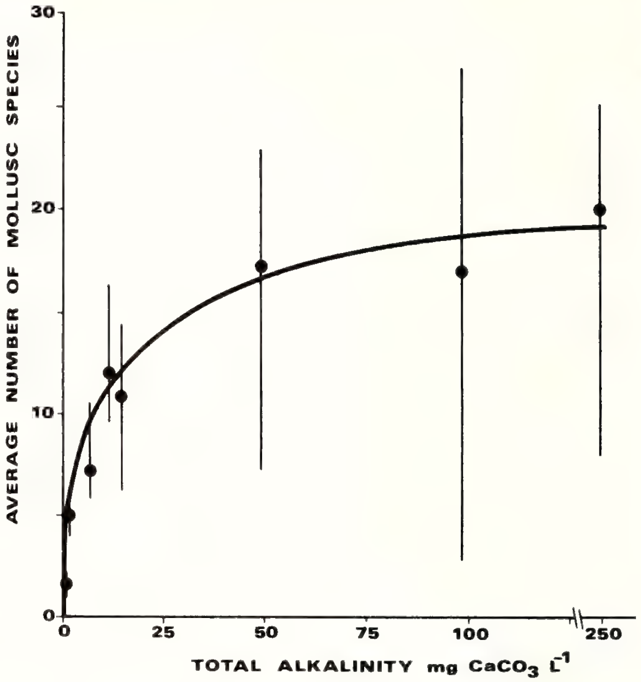

Fig. 7. Average number of mollusks species in relation to the total alkalinity of the environment. Data are from Mackie and Flippance (1983c).

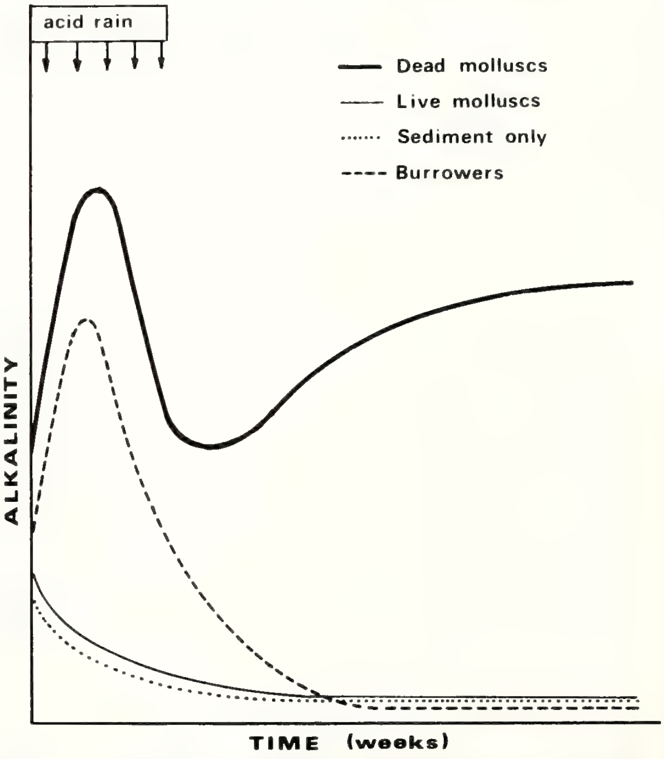

Fig. 8. Changes in alkalinities in aquaria containing either dead mollusks, live mollusks, sediment only, or burrowing dragonflies (*Gomphus*) and mayflies (*Ephemera*). Based on data in Rooke and Mackie (1984b).

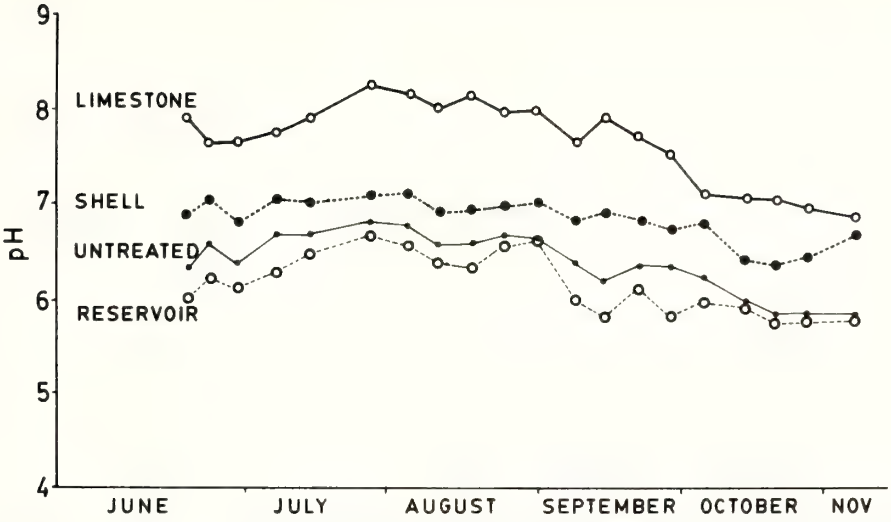

Fig. 9. Changes in pH over time in troughs containing either limestone, shells of *Elliptio complanata*, or no buffering material (untreated) using water from the outflow of Plastic Lake in south-central Ontario. The reservoir held water to maintain a pressure head before passing through the troughs. See Mackie *et al.* (1983) for details.

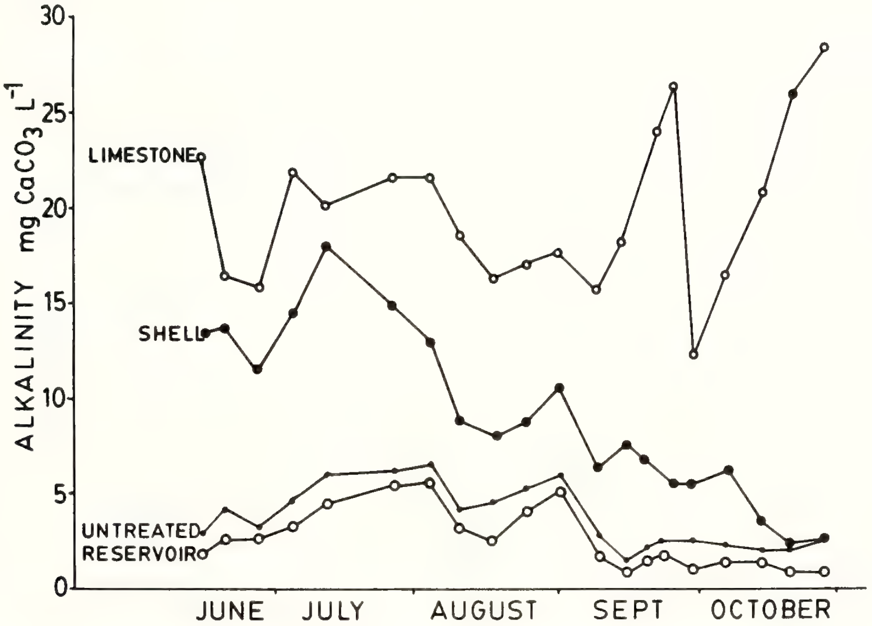

Fig. 10. Changes in alkalinities over time in troughs containing the same materials described for figure 9.

(*Elliptio complanata*) shells, and the third was untreated (i.e. control). The unionids were shucked and only the separated valves (with some remnants of adductor muscles attached) were used. Water from the outflow of Plastic Lake, an acidifying lake in south-central Ontario, was allowed to flow through the trough system and the changes in pH and alkalinity were recorded over time. Figures 9 and 10 show that the mollusk shells contributed some alkalinity but not as much as the limestone. Also, the limestone maintained a higher alkalinity than the mollusk shells after five months, even though there was still 90% of the calcareous shell material remaining. Shell dissolution could have been inhibited by the several layers of conchiolin that separate the nacreous layers of calcium carbonate. From this point of view, it could have been better to use shells of Corbiculacea species [e.g. *Corbicula fluminea* (Müller)] which lack internal conchiolin layers and dissolve more readily in acidic solutions (Kat, 1982). Moreover, the ammonia levels in the trough with mollusk shells rose to extremely high levels in the first few weeks of the experiment (Fig. 11), probably due to the breakdown of protein and ammonification of amino acids originating from residual adductor muscles on the inner valves of the shells.

The conchiolin layers could also have contributed to the ammonia levels.

CONCLUSIONS

In conclusion, the levels of hydrogen ions and metals in most acidifying lakes of southern Ontario are not great enough to directly eliminate the mollusks, but the present levels appear to be causing changes in shell composition, shell morphology, reproduction and growth that are sufficient to cause decreased production and diversity, and a change from a greater proportion of epifaunal grazers to infaunal, filter feeding mollusk communities.

ACKNOWLEDGMENTS

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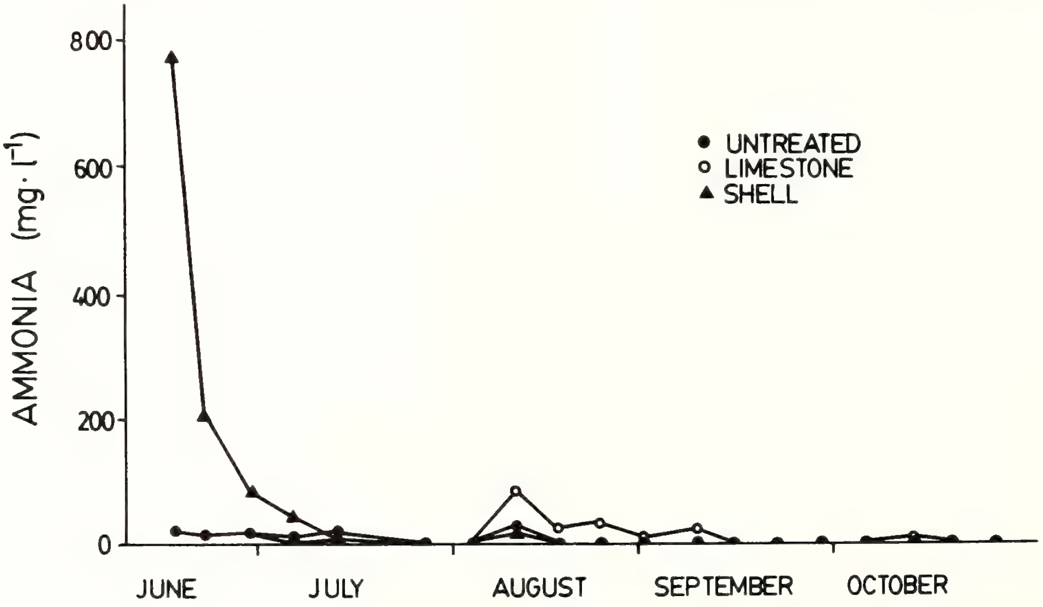

Fig. 11. Changes in ammonia concentrations over time in troughs containing the same materials described for figure 9.

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SEASONAL VARIATION OF SURVIVAL TIME IN ANOXIC WATER AND THE GLYCOGEN CONTENT OF *SPHAERIUM CORNEUM* AND *PISIDIUM AMNICUM* (BIVALVIA, PISIDIIDAE)

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ABSTRACT

I surveyed the ability of two freshwater bivalves, *Sphaerium corneum* (L.) and *Pisidium amnicum* (O. F. Müller), to survive anoxic water of different temperatures. Experiments using a small volume (2 to 5 ml water per 5-8 mm clam), closed-bottle method were run for over one year on individuals from small water bodies in eastern Finland. Total amount and location of glycogen in these bivalves was also examined by chemical analyses and histochemical methods.

Both species showed good ability for anaerobiosis. The 50% survival time for *Pisidium amnicum* was ca. 4.5 days at 20°C, but increased with decreasing temperatures, being almost 200 days at 0°C. *Sphaerium corneum* survived even better, with the corresponding survival times roughly twice as long at all temperatures. The results suggested that seasonal variation is not deducible from temperature alone.

Glycogen content of both species in nature varied seasonally between 0.5 and 3% glycogen per wet weight of tissue, with peak values attained in late autumn and early summer. The habitat of *Pisidium amnicum* was well oxygenated during winter, although part of the population overwintered in anoxia in ice or frozen sediment. The decrease in glycogen content during winter, and the seasonal variation in general, were more pronounced in clams experiencing anoxia. Ecological consequences of this anaerobic capacity and potential effects on the results of energetic studies are suggested to be important.

Small lakes and ponds in cold temperate areas commonly experience winter anoxia (e.g. Nagell and Brittain, 1977; Salonen *et al.*, 1984). This anoxia starts from the bottom sediments and a steep microstratification may often be found in the overlying water.

Consequently euryoxy, or capacity for facultative anaerobiosis (or even obligate, as in *Tubifex,* Famme and Knudsen, 1985), is common in benthic animals (Eggleton, 1931; Lindeman, 1942; Beadle, 1961; Seuss *et al.*, 1983). Examples include both marine and freshwater molluscs (De Zwaan, 1977, 1983, Gäde, 1983; Kluytmans and Zandee, 1983).

The tiny freshwater bivalves of the family Pisidiidae are relatively inactive, slow-moving infaunal animals. Since they are capable of neither "burst"-activity nor long migrations they are confined to certain areas of bottom sediment throughout their lives. As a result they must be able to tolerate all of the environmental variation present in these habitats, including anoxia. In addition to survival in anoxic water, a good capacity for anaerobiosis is of obvious value for Pisidiidae in aerial exposure, e.g. during passive dispersal (Mackie, 1979), aestivation in drying mud (Bleck and Heitkamp, 1980; McKee and Mackie, 1980) or wintering in ice (Olsson, 1981). Earlier reports of anoxia tolerance in Pisidiidae were given by Juday (1908), Jatzenko (1928), Eggleton (1931), Thomas (1963, 1965), Gale (1976), Way *et al.* (1980), Burky (1983) as well as Holopainen and Jónasson (1983). In addition, Dietz and Stern (1977) demonstrated a seasonal variation in carbohydrate content of *Sphaerium transversum* (Say). The aims of this study were to experimentally survey the ability of two common pisidiid species, *S. corneum* and *Pisidium amnicum*, to survive in anoxic water at different temperatures and in different seasons, and to examine the possible role of glycogen in this ability.

MATERIALS AND METHODS

Material was collected between August 1984 and August 1985 from the Siilaisenpuro River (*Pisidium amnicum*), and Lake Varaslampi (*Sphaerium corneum*), both situated in

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the town of Joensuu, in eastern Finland (62°37' N, 29°45' E). The river is about 3-4 m wide and 1.5-2.0 m deep at the sampling site. *P. amnicum* lives on the slopes in the soft bottom of mud and plant litter. Lake Varaslampi is oval with an area of about 3 ha and a maximum depth of about 4 cm. It is fringed by lush vegetation and has a thick mud deposit (4 m) in the deepest part. *S. corneum* was collected from the vegetation belt around the lake (open water period) and from the outlet ditch (during ice cover), where the population density was much higher than in the lake.

Both the river and lake are ice covered approximately 5 months (November - May) annually and have an annual temperature variation from 0.5 to 22°C (Fig. 1). Physical and chemical properties of the water are listed in Table 1. The oxygen content of the river water was high year round (min. 74% of saturation in March), whereas a severe depletion of oxygen in the lake caused a minor fish kill in April 1985. Total anoxia developed at a depth of 4 m in early December and reached the surface water in March. The sediment in the lake littoral probably experienced anoxia for 1-2 months during 1984-1985 winter. The outlet ditch stayed unfrozen for about 2 weeks in autumn and thawed again about 3 weeks earlier in spring, which may have considerably improved the oxygen availability in this site.

Both species were sampled by hand net at about 1 month intervals (with a 3 month pause in mid-winter). Samples were sorted and experiments were started on the same or following day. Adult clams of various sizes (5-8 mm) were placed in glass jars. River or lake water with very low oxygen content (< 0.5 mg/*l*) was then added. Bubbling with pure nitrogen for 1 hour was used to lower the oxygen content down to 0.5 mg/*l* or less. The volume of water per clam varied from 2 to 5 ml (5 to 10 clams in each jar with volume of 10-50 ml). The jars were then sealed with tight rubber or ground glass stoppers, covered with aluminium foil and immersed into constant-temperature baths. Every 1 to 4 days the jars were examined for dead animals. A clam was considered dead when its shell valve was open and the animal did not react to a shaking of the jar by closing its shell or withdrawing its foot. In addition, the heart beat of younger clams could be seen (and heart rate measured) through the glass by using a stereomicroscope and transmitted light. Initially, open vials were used as controls but because of almost no mortality in them, use of controls was later discontinued.

Table 1. Mean values of some physical and chemical properties of water in the study sites.

		Siilaisenpuro River	Lake Varaslampi
Conductivity	μmho/cm	110	220
pH		6.5	6.8
Color	Pt mg/l	110	70
COD_{Mn}	mg/l O_2	9.5	9.5
Tot. P	μg/l	106	75
Tot. N	μg/l	850	900
Ca	mg/l	12	25

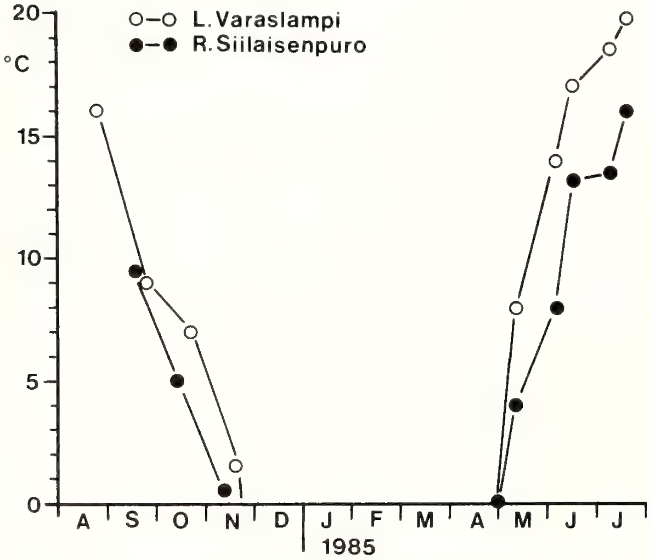

Fig. 1. The temperature of surface water in Lake Varaslampi and Siilaisenpuro River in the sampling dates.

Five to 15 clams were damp-dried on tissue paper, put into glass jars and stored deep-frozen at -40°C. The glycogen content of each individual was determined later by the method of Siu *et al.* (1970) and expressed as per cent of tissue wet weight (WW) (shell excluded). These can be converted to approximate values per tissue dry weight (DW) by multiplying by a factor of 8 for *Pisidium amnicum* (water 55% of WW and ash 85% of DW in intact clam) and 13 (water 72%, ash 80%) for *S. corneum*.

Additional clams were fixed in alcoholic Bouin, treated by the customary wax-embedding method, sliced and stained by Lillie's (1951) allochrome procedure to reveal glycogen concentrations.

For comparison, identical experiments were performed on samples from three additional populations of *Pisidium. Pisidium casertanum* and *P. subtruncatum* Malm were collected in September 1984 from 20 m in eutrophic Lake Esrom, Denmark, and *P. amnicum* from 0.5 m in oligotrophic Lake Pääjärvi were collected in March, May and June 1985.

In the Siilaisenpuro River, seasonal water level fluctuation caused the ice to contact the sediment during winter. In very shallow areas the sediment surface froze tightly to the ice. From this area (20-30 cm of water at the time of freezing) two ice clumps (680 and 1600 cm^2) were removed in March by chainsaw, and the frozen loose sediment on the bottom of the ice was rinsed and scraped away. The 30 cm thick pieces of solid ice with about 5 cm of frozen sediment enclosed were taken to the laboratory and thawed at 5°C. The material was then sieved and examined for living *Pisidium amnicum*.

RESULTS

BEHAVIOUR

The first reactions to sudden immersion in anoxic water were foot extension and increased locomotory activity. Within a few hours this changed to total inactivity and a tightly closed shell. *Sphaerium corneum* had longer periods of activity and, during the first few days, was often observed to crawl up to the roof of the vial. The clam then attached itself to the roof by a slime thread protruding from the middle of the foot slit and stayed hanging up. On several occasions this species also floated up in the vial, probably by a bubble (of unknown gas and origin) inside the shell. During the main period of anoxia pedal activity was rare and never the result of the shaking of the vial when regularly checked. On the other hand, an increase in temperature of several degrees (due to temporary power failures that occurred twice during winter) caused extension of the foot for some time in both species.

Even when heart rate was variable and sensitive to disturbance, the results suggested clear bradycardy during anoxia. At 9⁰ to 16⁰C the usual aerobic rate was 20-30 beats per minute in small *Sphaerium corneum, Pisidium casertanum* (Poli), and *P. subtruncatum*, whereas during long periods of anoxia, rates of only 1 to 2 beats per minute were often recorded. Sometimes no beats could be detected at all suggesting existence of even longer pauses. However, because of the imprecision of the method these results must be considered preliminary at present.

SURVIVAL TIME IN CLOSED VIALS

The experimental temperatures in autumn and early winter were chosen to be near ambient levels (Fig. 1) to reveal the actual capabilities of these species to survive winter anoxia in their specific habitat and to observe the development of the anoxic capacity. *Sphaerium corneum* survived almost 3 weeks at 16⁰C in August (Fig. 2A; further reference to time periods mean 50% survival). In September (at 9⁰C) this species was able to survive 72 days and in October-November as long as 150 days or more at temperatures of 7⁰C or below. The seasonal variation in temperature dependence of survival time can be seen in figure 3.

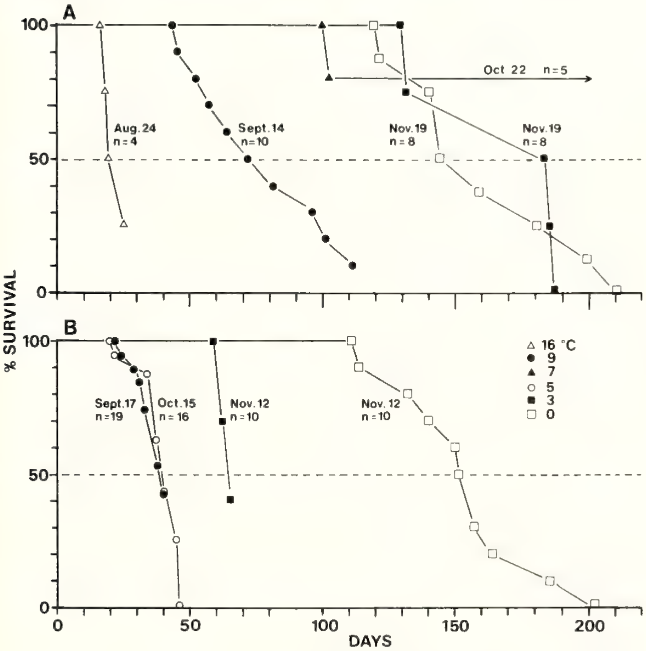

Fig. 2. An example of the survivorship curves of *Sphaerium corneum* (A) and *Pisidium amnicum* (B) in anoxia at different temperatures during autumn (August-November). The Oct. 22 experiment was interrupted after 201 days, when 4 of 5 clams were still alive. Numbers (n) denote individuals.

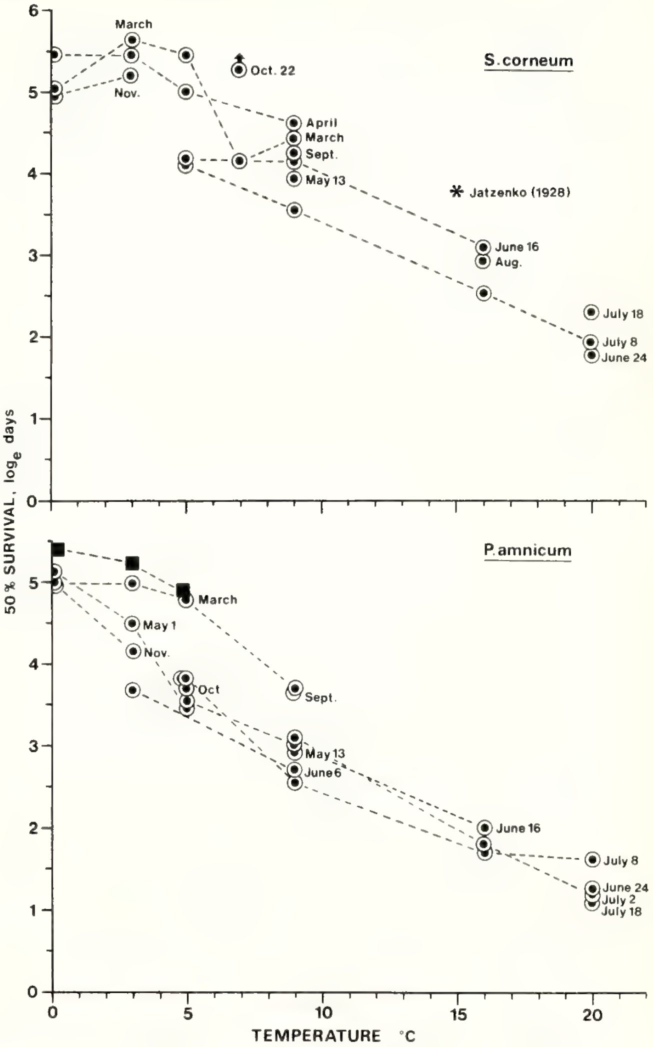

Fig. 3. The temperature dependence of the 50% survival time in experimental anoxia of *Sphaerium corneum* (A) and *Pisidium amnicum* (B). Results from the same sampling dates are connected by broken lines. Natural temperatures for each date are given in figure 1. The squares denote clams from Lake Pääjärvi collected in March 1985.

At 9⁰C the 50% survival time of *Pisidium subtruncatum* from Lake Esrom was 32 days (juveniles) and 36 days (adults; one adult survived 80 days). The single juvenile of *P. casertanum* died after 54 days whereas all three adults were alive when checked after 85 days of anoxia.

WINTERING IN ICE

The smaller ice block contained 4 living and 1 dead

Pisidium amnicum (73 individuals per m^2) whereas the larger contained 18 living specimens (113 per m^2).

GLYCOGEN CONTENT

The annual variation in total glycogen content is about 4-fold in both species (Fig. 4). Significant increases occurred in autumn (August - November) and in spring but decreases were observed during winter and summer.

The glycogen values for *Pisidium amnicum* thawed from the ice or taken from the shallow shore (0.2 m) are consistently lower (significantly in May, early June and July, analysis of variance, $P < 0.001$), than those collected only ca. 5 m apart from the depth of 1 m. The former probably overwintered in anoxic conditions in ice or frozen sediment (see below) and the latter in aerobic water. The same species from oligotrophic Lake Pääjärvi had a much lower glycogen content in March but showed an equal increase in early summer and a decrease in mid-summer.

There are some differences in the glycogen content between *Sphaerium corneum* from the outlet ditch and from the lake. In general, the seasonal variation seems to be more prominent (peaks are higher and minima lower) in the lake littoral, which probably had longer period of oxygen depletion than the outlet ditch. The differences between October (lake) and November (ditch) as well as the June values are not significant whereas in May and July the glycogen content of the ditch clams is significantly higher (ANOVA, $P<0.001$).

Histochemical techniques revealed a large deposit of glycogen granules in the subepithelial tissue of the foot in both species and in the mantle of *Sphaerium corneum* during winter. Some glycogen can also be seen in the gill (Figs. 5 and 6). On 1 May, five large specimens of *Pisidium amnicum* were relaxed by pentobarbital (Meier-Brook, 1976), the soft tissue was dissected into five different components and the glycogen content of each component was determined after drying at 60°C for 12 hrs. The glycogen contents were as following: foot 13.6% of tissue DW, mantle 12.7%, gills 11.9%, digestive diverticulae 4.3% and the rest 11.9%, yielding a weighted mean of 11.1%. The coincident mean value determined as percent of WW (1.47 ± 0.261) was in agreement. The content of the foot is not much higher than the other components probably because of the relatively low overall content at that time (the glycogen content in Fig. 6 is twice as high).

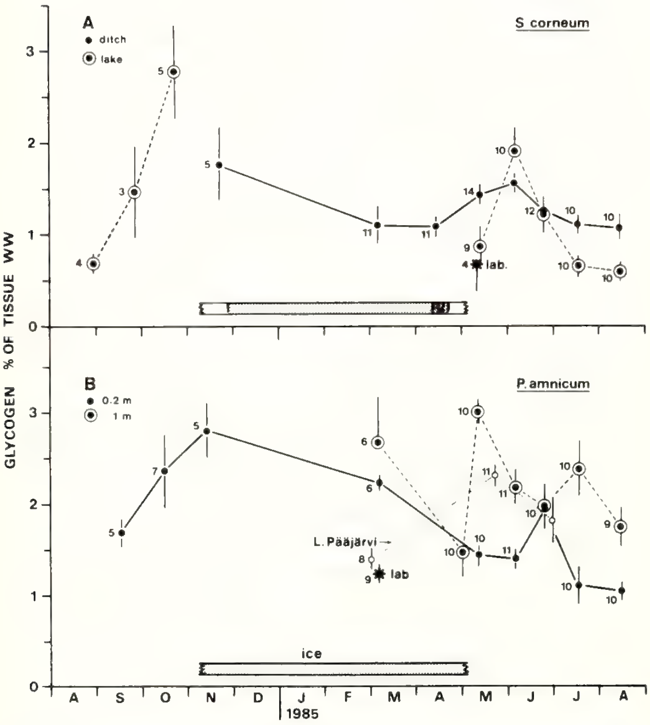

Fig. 4. The seasonal dynamics of total glycogen content (% of tissue wet weight, WW) in *Sphaerium corneum* (A) and *Pisidium amnicum* (B). Part of the samples in (A) came from lake littoral (0.5 m) and part from the outlet ditch (0.5 m, ca. 50 m from the lake). The asterik shows the glycogen content of clams sampled on 22 October 1984 after 201 days of laboratory anoxia at 7°C. In the ice-cover the shaded period in A refer to the outlet ditch (partial ice-cover in spring). Figure (B) includes samples from two depths in the Siilaisenpuro River (clams in the March sample from 0.2 m were frozen in ice) and three samples from the littoral (0.5 m) of Lake Pääjärvi, southern Finland. The asterisk shows glycogen content after 114 days at 3°C in a small volume of water in the laboratory (November sample in open bottle).

DISCUSSION

The most common response to anoxia is inactivity, including prominent bradycardy (e.g. De Zwaan, 1977). According to Gale (1976), heart rate in *Sphaerium transversum* slows down to "only a few times a minute" in anoxia, with which my results agree. Lowered metabolic rate, down to 5-10% of aerobic levels, is generally thought to be necessary in anoxia in order to save energy stores, because of the inefficiency of anaerobic metabolism (Zs. -Nagy, 1973; Gnaiger, 1983). The upward crawling response exhibited in this study by *S. corneum* would, in its habitat among aquatic vegetation (e.g. Zhadin, 1952), be advantageous in avoiding anoxia, although it might also increase the risk of predation. It is not known if this species naturally overwinters up out of the sediment, with the shells fixed by slime threads to aquatic macrophytes. A similar secretion of slime threads has been previously described [e.g., Zhadin (1952) and Ellis (1978)].

The survival times given here must be considered as minima because of the probable adverse effects of the small-volume closed-bottle method used. The accumulation of metabolites, H_2S and the effects of decaying specimens probably reduced survival even at low temperatures, although H_2S is often also present in nature. In this study the recovery of the individuals with closed shells was almost 100%, when measured by the ability to begin locomotion after transfer to aerobic water. This ability, however, would not guarantee the survival of the exhausted clams under natural conditions. Yet the survival times given here equal or exceed many of the scattered values given previously for molluscs and are of great enough length to have significant ecological implications.

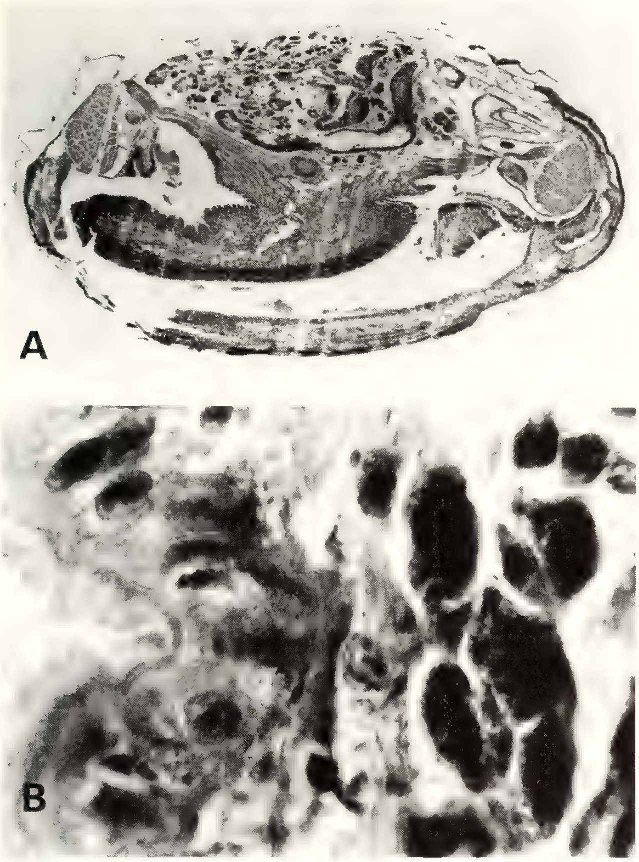

Fig. 5. (A) A median section of *Pisidium amnicum* collected from Siilaisenpuro on 5 March 1985. High concentrations of glycogen in the subepithelial tissue of the foot is shown by black color. Allochrome HFW = 5.5 mm. (B) Ventral surface the foot of *P. amnicum* showing a epithelial cilia and subepithelial cells filled with glycogen granules. Allochrome HFW = 0.05 mm.

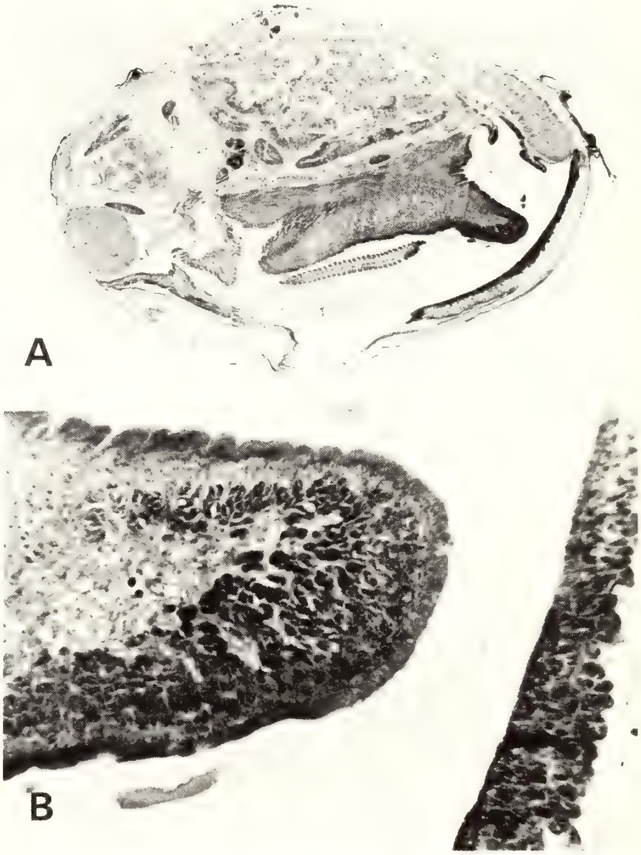

Fig. 6. A median section of *Sphaerium corneum* collected from Lake Varaslampi on 5 March 1985. Glycogen is seen as prominent black areas in both the foot tip and mantle with some reaction in the gill, also. Allochrome (A) HFW = 7 mm and (B) HFW = 0.7 mm.

Survival times of up to 55 days at 10°C have been reported for marine molluscs (Theede *et al.*, 1969; Hammen, 1976). Zs.-Nagy (1973) gives 7-10 days as the anoxia tolerance period for *Anodonta cygnea* (L.) at 15°C; *Ligumia subrostrata* (Say), another freshwater species, survived more than 15 days at 25°C (Dietz, 1974). These are, however, short times when compared to aerial survival of one year or more of some tropical unionids at very high temperatures (Dance, 1958).

I also held a juvenile *Anodonta piscinalis* Nilsson (= *A. cygnea*) (30 mm, caught in March from Lake Pääjärvi), 66 days in anoxic water at 3°C. When transferred to aerobic water, the foot was soon introduced but started to withdraw upon touching only after 1 day.

Indications of the survival of Pisidiidae during anoxia in natural lakes range from 2-3 months (Juday, 1908; Holopainen and Jónasson, 1983) to 5-7 months (Eggleton, 1931). In addition, some experimental data are given by Juday (1908), Jatzenko (1928) and Eggleton (1931). My data on *Sphaerium corneum* closely agree with the 46-day survival time at 14-16°C reported by Jatzenko (1928) (see Fig. 3).

Besides temperature, survival times in anoxia probably depend on season, animal size and physiological state, as well as the possible existence of poisonous compounds (like H_2S) in the water. In my experiments the existence of H_2S was often suggested by black coloration on the shells and the odor emitted when the vials were opened. Zhadin (1952) reports *Sphaerium corneum* to be resistant to H_2S and to survive 14 days at 30mg/*l* of H_2S. Theede *et al.* (1969) and Shumway *et al.* (1983) have shown the deleterious effect of this compound on survival times of marine invertebrates.

Since only adults were used in most experiments, the effect of size could be examined only in case of *Pisidium casertanum* and *P. subtruncatum* from Lake Esrom. In both species juveniles appeared to die first. However, survival times of these species were long considering that at the time of sampling (September) they had already survived several weeks of anoxia in Lake Esrom (Holopainen and Jónasson, 1983).

The effects of temperature on survival times are prominent and appear linear on semi-log scale (Fig. 3). The average 50% survival time of *Pisidium amnicum,* which is about 4.5 days at 20ºC, increases up to 200 days at 0ºC. The survival times of *Sphaerium corneum* are roughly twice as long at all temperatures. This seems to be in accordance with the habitat choice of these species. *P. amnicum* is an inhabitant of sandy bottoms of large lakes and prefers flowing water whereas *S. corneum* prefers muddy bottoms in small ponds and more nutrient-rich rivers (the Siilaisenpuro River also has a sparse population of *S. corneum*).

In this survey the effects of season (seasonal changes in the physiological state of the clams) can not be clearly separated from the effects of temperature alone. In figure 3, however, some difference in survival ability between winter and summer is obvious and is probably a reflection, in part, of the seasonal changes in enzyme activity patterns and carbohydrate or lipid store dynamics. The temperature dependence could be influenced by the method, if the accumulation of metabolites in water is the main cause of death. At high temperatures the deleterious levels will soon be achieved in a small bottle.

Anoxic energy metabolism is based entirely on carbohydrates and stores of glycogen are a necessary prerequisite for sustained life without oxygen. This energy deposit, however, is probably not limiting and the seasonal dynamics appear in many species to be connected to other activities (growth, reproduction) rather than anoxia tolerance (De Zwaan, 1977; Zs.-Nagy and Galli, 1977; Dietz and Stern, 1977; Zandee *et al*., 1980). However, in my results a clear depletion of stores is seen during winter, especially in anoxic conditions (Fig. 4).

The results of Zandee *et al*. (1980) on *Mytilus* show a high glycogen content (30-35% of DW) during the entire winter and a rapid decrease to 5% just before spawning in April. The dynamics of lipid content were reversed. Zandee *et al*. (1980) found highest concentrations of glycogen from the mantle and the "rest" (including the foot), whereas De Zwaan and Zandee (1973) reported only low values for the foot and muscles (half of that found in the mantle). My results for *Sphaerium corneum* resemble the dynamics of carbohydrate content of *S. transversum* (Dietz and Stern, 1977) by having a similar range (4 x) and a peak value in November; the glycogen content of *S. corneum* is however, ca. 50% higher.

In addition to overwinter glycogen consumption, the dynamics in glycogen content in pisidiids probably depends on the seasonal cycle of growth and reproduction as well. The population dynamics of *Sphaerium corneum* in Lake Varaslampi is not known but *Pisidium amnicum* in the Siilaisenpuro River gives birth in July and new eggs are laid in August, but the embryos stay small until the following May. The increase in glycogen content in spring coincides with increase in oxygen, temperature and food availability as well as the start of both adult and embryo growth again. The drop in mid-July could be due to the release of embryos at that time. In *Mytilus* the carbohydrate metabolism is replaced by lipid metabolism in midsummer (Zandee *et al*., 1980) but this has not been shown in pisidiids. In late summer and autumn the rebuilding of winter stores is again seen as an increase of glycogen.

Wintering within ice requires cold-hardiness even with the insulation of snow (about 50 cm) and ice. The long period of exceptionally cold weather (mean monthly air temperatures in January and February 1985 in Joensuu were -21.2º and -19.8ºC, respectively) must have lowered the temperatures inside ice well below zero. However, *Pisidium* spp. have been shown to tolerate subzero temperatures, e.g. after 4 months at an experimental temperature of -4ºC, the survival of *Pisidium* spp. was 57% (Olsson, 1981). The overwintering abilities of *Pisidium* and many other invertebrates in ice has long been known (Nordenskiold, 1897, Grimås, 1961, Holmquist, 1973) but the quantitative importance of it has been only recently understood (Olsson, 1981).

Ice provides a refuge from predation, which in some cases may more than compensate for the risk of fatal freezing. In the Siilaisenpuro River, probably more than half of the total *Pisidium amnicum* population live in the shallow areas and is susceptible to freezing.

In spite of limitations set by the simple method (small volume of closed bottle, no acclimation, exact clam volume/water volume ratio unknown) the results of this survey emphasize the importance of anaerobiosis for these species. The survival times are long enough to allow 6 months anoxic wintering and even at 20ºC the 5-10 days survival times allow considerable distances to be covered in passive dispersal.

Presently the capacity for anaerobiosis of molluscs (including Pisidiidae), as well as the physiological basis of this ability, are much better known than the ecological consequences. For example, metabolic rates of molluscs in severe hypoxia can be greatly suppressed (down to 5-10% of normal, e.g. De Zwaan, 1977), and even in the presence of oxygen, the contribution of anaerobic metabolism to total energy yield can be considerable (e.g. Famme *et al*., 1981). I suggest that these facts should be more seriously considered in all energetic studies on molluscs, especially in productive habitats that have great daily and/or seasonal variation in water oxygen pressure.

The two species of the present study seem to use their capacity for anaerobiosis only in order to tolerate the anoxic periods between more favorable conditions. Interestingly, a case of self-induced anaerobiosis (Taylor, 1976) and even obviously anoxic modes of life (Thomas, 1963, 1965; Way *et al.,* 1980; Shumway *et al.,* 1983) have been reported for some bivalves. In the latter cases productive environments and completely different behavioural responses are needed to ensure sufficient food intake for requirements set by elevated rate of glycolytic processes with their low efficiency in energy conversion.

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ENVIRONMENTAL INFLUENCES ON LIFE HISTORY TRAITS IN *PISIDIUM CASERTANUM* (BIVALVIA: PISIDIIDAE): FIELD AND LABORATORY EXPERIMENTATION

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ABSTRACT

This study reports on the factors that influence life history variation in the clam *Pisidium casertanum* (Poli). Monthly samples of > 100 individuals were taken from June 1982 through May 1983 from two ponds in southwest Virginia. Riopel Pond (RP) has a lower calcium content, alkalinity and is more oligotrophic than Farriers Pond (FP). Clams from FP reach a larger maximum shell length than those from RP. Both populations produced two generations per year: a summer generation in June and a fall generation in August-October. Differences in life-span, age at first reproduction, embryonic mortality and developmental rate and fecundity between the two populations were noted. A principal components analysis on these and published data indicates that both habitat predictability and favorableness are important factors shaping the variability in life history traits in this species.

Transfer experiments conducted to assess whether environment or genotype was responsible for the differences in life histories indicate that, based on survivorship patterns, individuals are well adapted to their own ponds and that those from a harsher habitat (RP) thrive in a more favorable habitat (FP) while the reverse tranfer results in poor survivorship. There were also differences in birth rates among transfers, with the results indicating there is an environmental component to the differences in birth rates.

To assess whether calcium availability or alkalinity was a factor involved in explaining the differences noted in life history, clams were cultured in the laboratory under varying water hardnesses utilizing pond water (from either FP or RP) as controls. The results suggest that there are both environmental (water hardness) and genetic (pond of origin) components to life history variation.

Preliminary starch gel electrophoresis on four enzyme systems indicated that there was a difference in genetic makeup of the two populations. All individuals examined from RP had the same genotype while there were a number of genotypes represented in the FP population, including the RP genotype.

A number of models of life history evolution have been put forth [e.g. r and K-selection, bet-hedging, adversity selection etc. (see Stearns, 1976, 1977; Parry, 1981; Greenslade, 1983)]. Brown (1985a) and Way (1985) have recently emphasized the need for intraspecific comparisons of life history "tactics" since intraspecific variation can most easily be used to examine the proximate selection pressures that have led to various tactics. Also, Stearns (1983, 1984) indicated that much of the variation in life history traits noted at higher taxonomic units can be explained by variation in body size and that many of the differences once noted in life history traits are not significantly different if body size is used as a covariable. Consequently intraspecific comparisons of life history tactics can be more valid. One objection to utilizing intraspecific comparisons, however, is that much of the variation observed in life history traits between populations can be due to environmental variation rather than to genotypic differences and thus selection would have no role in explaining the observed differences (see e.g. Stearns, 1980). It is well known that there is a great deal of phenotypic plasticity displayed by freshwater molluscs (see Russell-Hunter, 1978; Burky, 1983; Russell-Hunter and Buckley, 1983) but the relative importance of genotype versus environment in accounting for this plasticity is relatively unknown. The extensive work by Brown (1979, 1982, 1983, 1985a, b) on life history variation in pulmonate snails is one of the few studies where the role of genotype and environment is examined in explaining the differences noted in life histories in molluscs, although other workers (e.g. Browne *et al.*, 1984; Pace *et al.*, 1984; and papers in Dingle and Hegmann, 1982) have dealt with these problems in other taxa.

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Little work has been conducted on life history evolution in the freshwater bivalves of the family Pisidiidae. Studies by Way *et al.* (1980), Hornbach *et al.* (1980b, 1982), Way and Wissing (1982), McKee and Mackie (1981) and others (reviewed by Burky, 1983) have examined life history variations in this group by comparing the population structures of various species in contrasting environments. None of these studies, however, have attempted to experimentally test whether the noted variations in life history are environmentally or genetically induced. In the present study we examine life history variation in two populations of the freshwater pisidiid clam *Pisidium casertanum* (Poli). This species of clam is probably the most widespread of any freshwater mollusc. It is found on all continents (except Antarctica) and has been collected from ephemeral habitats, ponds, streams and both the littoral and profundal regions of lakes (Herrington 1962; Clarke 1973; Burch 1975; Mackie *et al.*, 1980). In addition, considerable variations in life history have been reported for this species with life spans ranging from < 1 to 5 years, brood size varying from 8 to 33 young per adult and with the number of generations produced per year varying from 1 to 2 [see e.g. Heard (1965); Mackie (1979); Holopainen and Jonasson (1983); this study].

The goals of this study were: 1. to quantify intraspecific differences in the life histories of *Pisidium casertanum*; 2. to assess, through transfer experiments and electrophoretic analysis, whether the differences noted in life histories could be accounted for based on variation in genotype or if environmental influences were most important; and, 3. to assess, through laboratory experiments, whether calcium availability (or alkalinity) was an important environmental factor influencing the variation in life history traits.

MATERIALS AND METHODS

LIFE HISTORY TRAITS

Pisidium casertanum for this study were collected from two ponds in southwest Virginia (both near Mt. Lake Biological Station). The ponds are very similar in surface area and volume but differ quite significantly in their water chemistry (Table 1). Riopel Pond (RP) is an extremely soft water, low alkalinity pond located on the top of Salt Pond Mountain. It has a very small drainage basin mainly of igneous rock outcrops. Farriers Pond (FP) is located at the base of Salt Pond Mt., has a higher ionic content and a larger drainage basin which includes some sedimentary outcrops. RP is a sterile pond with few benthic invertebrates or macrophytes while FP is a much more diverse system. The low O_2 availability in FP during the summer (Table 1) attests to the more productive nature of this pond when compared to RP.

Table 1. Physical and chemical characteristics of two pond habitats of *Pisidium casertanum* (chemical methods according to APHA, 1980).

	Farriers Pond	Riopel Pond
Altitude (m)	595	1164
Maximum Depth (m)	4.5	4.0
Surface Area (m^2)	6729	6432
Volume (m^3)	13498	8234
Dissolved Oxygen[1] (July)		
(mg/*l*	3.7	8.2
% saturation	49	109
Total Alkalinity[2] (July)		
(mg/*l* as $CaCO_3$)	105	2
Hardness[3] (July)		
(mg/*l* as $CaCO_3$)		
Ca	82.4	4.0
Mg	47.4	2.0
Conductivity[4] (μmhos)		
June - July	279	10
March	230	17
pH[5]		
July	6.9	4.6
March	4.8	5.0

1. Azide-modified Winkler titration
2. Titration with brom-cresol green methyl red indicator
3. Titration with EDTA
4. YSI Model 33 S-C-T meter
5. Orion model 221 pH meter

Clams were obtained from the substratum by washing through 0.5 mm sieves. Usually, samples consisted of > 100 clams which were fixed in the field in 12% neutral formalin. Shell lengths were measured (anterior to posterior dimension) to the nearest 0.1 mm using a dissecting microscope with a stage mounted micrometer for clams < 2.5 mm and with a vernier caliper for clams ≥ 2.5 mm. Examination of the time-series of shell length frequency diagrams allowed for the determination of seasonal shifts in population structure. By examining shifts in shell length frequency diagrams, and through the use of probability paper (Harding, 1949; Cassie 1950, 1954) to examine the polymodal distributions, and with the reproductive data on this population (see below), it was possible to assess the population dynamics of *Pisidium casertanum* from these two ponds.

To assess the reproductive status of the population, approximately six adults were dissected from each collection period to examine for the presence of embryos. Embryos were removed from gravid animals, counted, and their length measured to the nearest 0.1 mm using a dissecting microscope with a stage-mounted micrometer. Pisidiid clams are ovoviviparous (Mackie, 1978) and brood young in marsupial sacs on their gills. In the genus *Pisidium* only one ontogenetic stage [embryo, fetal larvae, prodissoconch larvae or extramarsupial larvae (see Okada 1935, 1936)] is found in a given individual. By examining the seasonal changes in the size distribution of embryos found within adults, it is possible to assess for periods of reproductive output and to estimate embryonic development rates (see Hornbach *et al.*, 1980b, 1982). Dissection of only six clams provides a general view of the reproductive dynamics in these populations. Additional dissections are needed to provide quantitative estimates of reproductive output in the genus *Pisidium* because of the considerable variability in the number of reproductively active adults in these populations (Way, pers. comm.).

In July 1982, a number of clams were removed from the two ponds to examine whether there were differences in the inorganic content (mostly $CaCO_3$) of clams of various sizes. Whole clams were dried to constant weight at 100°C and then ashed at 500°C. The difference in weight before and after ashing is taken as the ash-free dry weight, an indicator of organic content.

TRANSFER EXPERIMENTS

To assess for the relative contribution of environment and genotype on phenotypic variability displayed in these clams, individuals were transferred between ponds from late June 1982 through early December 1982. Transfer cages consisted of plastic boxes (17.5 cm x 31.5 cm x 8.0 cm) into which 1.4 cm plastic petri dishes had been cemented. Approximately 5 clams of each of 4 size categories ($\leq$ 1.2 mm, 1.3-2.0 mm, 2.1-2.5 mm and $>$ 2.5 mm) were placed in the dishes. The dishes were then covered with 0.3 mm nylon mesh. There were 4 levels of treatment in the transfer experiments: 2 controls and 2 tranfers. The controls were clams taken from a given pond and then maintained in that pond. Clams from RP maintained in RP are denoted RP→RP. Clams from FP maintained in FP are denoted FP→FP. The transfers were clams taken from one pond and maintained in the other pond. Clams from RP maintained in FP are denoted RP→FP. Clams from FP maintained in RP are denoted FP→RP. Approximately 8 replicate dishes of 5 clams per dish of each of the 4 size categories of clams were used in each treatment. Approximately every 2 weeks from the period late June through late August, and then monthly thereafter, the transfer cages were removed from the ponds and survivorship, growth (as increase in mean shell length) and reproductive output (the presence of newborns in the containers) were assessed.

LABORATORY EXPERIMENTS

In order to examine the influence of calcium availability (or alkalinity) on life history traits of *Pisidium casertanum*, 10 small ($\leq$ 1.2 mm) clams from either FP or RP were placed in small (150 ml) plastic containers with either filtered (0.45 μm) pond water (from FP or RP) or very soft, soft, hard or very hard water (made according to APHA, 1980 guidelines for reconstituted water). Water hardness was 10-13, 40-48, 160-180 and 280-320 mg l^{-1} as $CaCO_3$ while total alkalinity was 10-13, 30-35, 110-120 and 225-245 mg l^{-1} as $CaCO_3$ for very soft, soft, hard and very hard water, respectively (APHA, 1980). The number of replicates varied from 3 to 20 for each treatment. Water levels in the containers were maintained by adding distilled water. Clams were fed 0.1 mg of ground Tetra-Min^R fish food per clam per day. The amount of calcium added by the fish food to the containers is unknown. At monthly intervals, the water was changed and clams were removed and their shell lengths measured to assess for growth. Survivorship and births in the chambers was noted on a regular basis. These experiments were begun in late June 1982 and were continued until all original clams used in the experiments were dead (December 1984).

ELECTROPHORESIS

A preliminary examination of the genetic structure of the two populations of *Pisidium casertanum* was performed utilizing horizontal starch gel electrophoresis. Clams were obtained from the ponds and were ground in equal volumes of tris HC1 buffer (pH 7.0). Attempts were made to examine 11 enzyme systems: ADH, CAT, EST, GOT, IDH, LAP, MDH, ME, PEP, PGI, and PGM, (see Werth, 1985 for methods). Only four of these systems (EST, PEP, PGI and PGM) were sufficiently resolved to be used in genetic analysis. Based on the distribution of the alleles of various loci for each system, Nei's (1972) genetic distance was calculated between the two populations.

RESULTS

LIFE HISTORY TRAITS

The populations of *Pisidium casertanum* that inhabit Farriers Pond (FP) and Riopel Pond (RP) displayed quite different population structures. Clams from FP collected from June 1982 to May 1983 ranged in size from 0.7 to 4.8 mm (Fig. 1). Clams collected from RP from this same time period, however, ranged in size from 0.6 mm to only 3.3 mm with most having an upper size of 2.6-2.8 mm (Fig. 1). This indicates that on the average clams from RP reach a maximum size which is approximately 40% less than clams from FP.

It is not readily apparent from figure 1 when the periods of major reproduction are occurring in these two ponds. Results from the dissection of adults for the assessment of reproductive condition, however, do give indications of the timing of reproduction in these two ponds (Fig. 2). In both ponds larvae that reach a size of approximately 0.7 mm are extramarsupial (those able to be born). Inspection of figure 2 shows that in RP extramarsupial larvae are found in parents in June, July, early August and October. In FP, they are found during May, June and October. In both ponds there seems to be two periods of peak reproductive activity, summer and fall with a late-summer, early-fall period of reduced reproductive activity.

Despite the fact that the two populations show similar birth periods, there are differences in the timing of reproductive activity. In FP, reproductive activity appears to begin earlier in the year than in RP. This could be due to the earlier spring increase in temperature at FP due to its location at

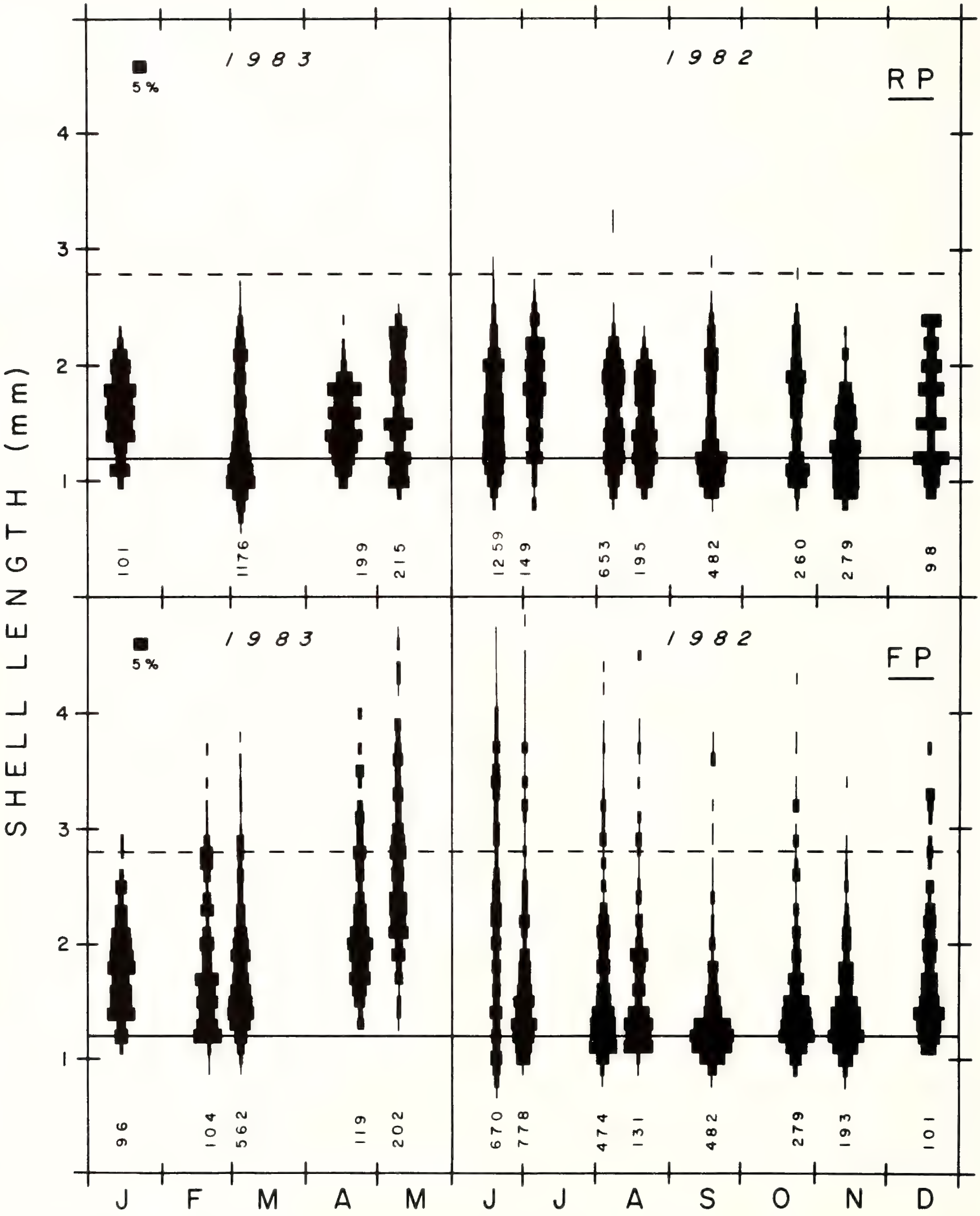

Fig. 1. Shell length-frequency diagrams for the period June 1982 - May 1983 of *Pisidium casertanum* from two ponds in southwest Virginia (Riopel Pond - RP and Farriers Pond - FP). Solid horizontal line shows the maximum size at birth (1.1 mm) and the dashed horizontal line at 2.8 mm is provided as a reference to highlight the differences in maximum shell lengths attained by the two populations. Numbers under the histograms are sample numbers. Data for January - May 1983 were plotted before the June - December 1982 data to facilitate the observation of annual trends. This assumed little year to year variation in population dynamics.

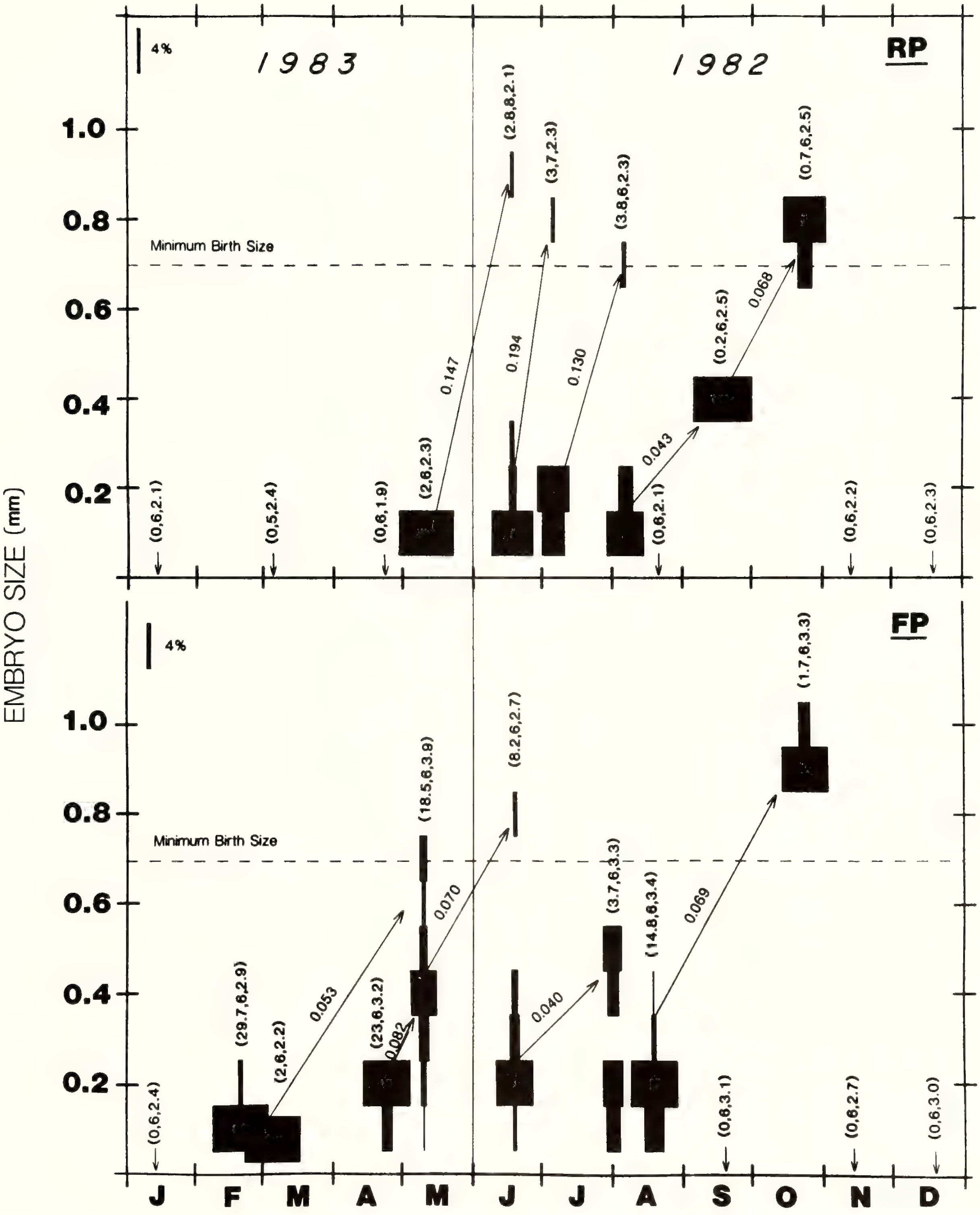

Fig. 2. Embryo size-frequency diagrams from adult *Pisidium casertanum* for the period June 1982 - May 1983 from two ponds in southwest Virginia (Riopel Pond - RP and Farriers Pond - FP). Numbers in parentheses are the mean number of embryos per adult, the number of adults dissected, and the mean shell length of the adults dissected, respectively. The arrows give the probable dynamics of embryonic development and the numbers on the arrows indicate the embryonic development rates in mm per week. Data for January - May 1983 were plotted before the June - December 1982 data to facilitate the observation of annual trends. This assumed little year to year variation in population dynamics.

a lower elevation. Also there are differences in the size of adults which can contain extramarsupial larvae. The smallest clam which contained extramarsupial larvae was 1.7 mm from RP and 2.3 mm from FP. There were also differences in the rates of embryonic development (arrows in Fig. 2), especially during the summer. In RP, developmental rates during May and June seem to be about twice as high as rates for embryos from FP. This could be due to the fact that clams from RP must reach their birth size in a shorter time period and may also be responsible for some of the differences in the number of embryos produced (see discussion below). The embryonic development rates do not however appear to be significantly different between the two ponds for the late summer and early fall reproductive periods. Despite differences in the timing of reproductive activity, both populations appear to produce newborns at the same time; in early summer (summer generation - SG) and in late-summer or early fall (fall generation - FG) (Figs. 1-3 and discussion below).

Potentially more important than the minor differences in timing are the quantitative differences in reproductive output. At all times of the year adults from FP contain more embryos than adults from RP (see numbers in parentheses in Fig. 2). Univariate analyses of variance (Table 2) indicate that there is a significantly larger number of small and medium-sized embryos from adults from FP when compared to RP. This is true even when adjusted for the differences in the sizes of adults from these ponds as no significant pond by shell length interaction is indicated (Table 2). Of great interest is the fact that there is a significant difference in the number of size 1 embryos (0.1 mm) produced between the two ponds. This would tend to indicate that there is a difference in fecundity. The fact that there is no significant difference in the number of large (extramarsupial) embryos in adults from the two ponds could indicate that while there is a significant difference in fecundity (number of size 1 embryos produced), there is also a difference in embryonic mortality which results in similar numbers of young actually being born. It is just as likely, however, that in our dissections of adults we missed a large number of extramarsupial larvae that were produced because they were born and were not retained within their parents.

By combining data on reproductive output (Fig. 2), and the seasonal shifts in shell length frequency patterns (Fig. 1) it was possible to construct the most probable patterns of the population dynamics of *Pisidium casertanum* from these two ponds (Fig. 3). In FP, clams are born in the summer (June = summer generation - SG) or in late summer to early fall (August-October = fall generation - FG). Those individuals born in the summer grow and some reach reproductive size (2.3 mm) by late October. These individuals probably do not contribute significantly to fall reproduction because of their marginal size and the fact that this size is not reached until late in the reproductive season. These SG clams do, however, contribute significantly to the following year's summer reproduction and a few can survive to contribute to fall reproduction. The summer generation then has a life span of 12-16 months and can reproduce twice during their life. The fall-born generation, however, can live 20-22 months and probably contribute to three reproductive periods (the summer following their birth, then fall and potentially a small reproductive contribution in a second summer season). Whether these two generations remain completely separate is probably unlikely because of individual variations in growth rates.

The pattern of growth and reproduction in RP is similar in many aspects to the pattern discussed for FP. There are again two major periods of birth; summer and fall. In RP, however, the summer generation probably reaches sufficient size (1.7 mm) early enough in the fall to contribute to this period of recruitment. Thus, clams from the SG of RP are capable of reproducing at a younger age (4-6 months) than SG clams from FP. The summer-born clams from RP have a similar life span to the SG from FP (12-14 months) but with the earlier age of first reproduction they can potentially reproduce three times in their life span rather than twice as for the SG clams from FP. The fall-born clams from RP have a life span of approximately 20 months and can also be able to reproduce three times in their life.

In addition to the difference in the patterns of growth and reproduction noted in these two populations, there are differences in the energy content of clams from RP and FP. Regressions of the $\log_e$ (shell length-SL) on $\log_e$ (ash-free dry weight-AFDW) resulted in the following equations:

for RP: $\mathrm{AFDW} = 0.033\ \mathrm{SL}^{2.123}$ ($r^2 = 0.7$, $N = 58$);

for FP: $\mathrm{AFDW} = 0.024\ \mathrm{SL}^{2.649}$ ($r^2 = 0.8$, $N = 57$).

Analysis of covariance indicates that the exponents of these equations are significantly different ($F = 4.38$, $df = 1, 113$, prob $F = 0.040$). This indicates that clams of the same shell length can have different ash-free dry weights. In fact, inspection of figure 4 shows that smaller clams from FP have a lower percentage of their total dry weight as organic matter, or a higher percentage of their weight as inorganic matter (probably $CaCO_3$). This is not surprising given the fact that there is a much greater calcium availability and total alkalinity in FP (Table 1).

TRANSFER EXPERIMENTS

The transfer experiments lasted from July through December 1982. During this period there was little (< 0.1 mm) or no growth in any of the transfer chambers (potentially a chamber effect). There were, however, differences in survivorship and reproductive outputs in the various treatments. Within any transfer experiment larger clams generally had greater survivorship than smaller clams (Table 3). Of particular interest, however, is the effect of the transfer on survivorship within any size group of clams (Fig. 5). For each size group there are significant differences in the survivorship curves (based on the Breslow statistic, see Dixon and Brown, 1979). In most cases the control groups (FP → FP and RP → RP transfers) showed the highest survivorship. Clams transferred from RP to FP also showed good survivorship while those transferred from FP to RP displayed the poorest survivorship. These data indicate that clams from both FP and RP are well adapted for their own environments and

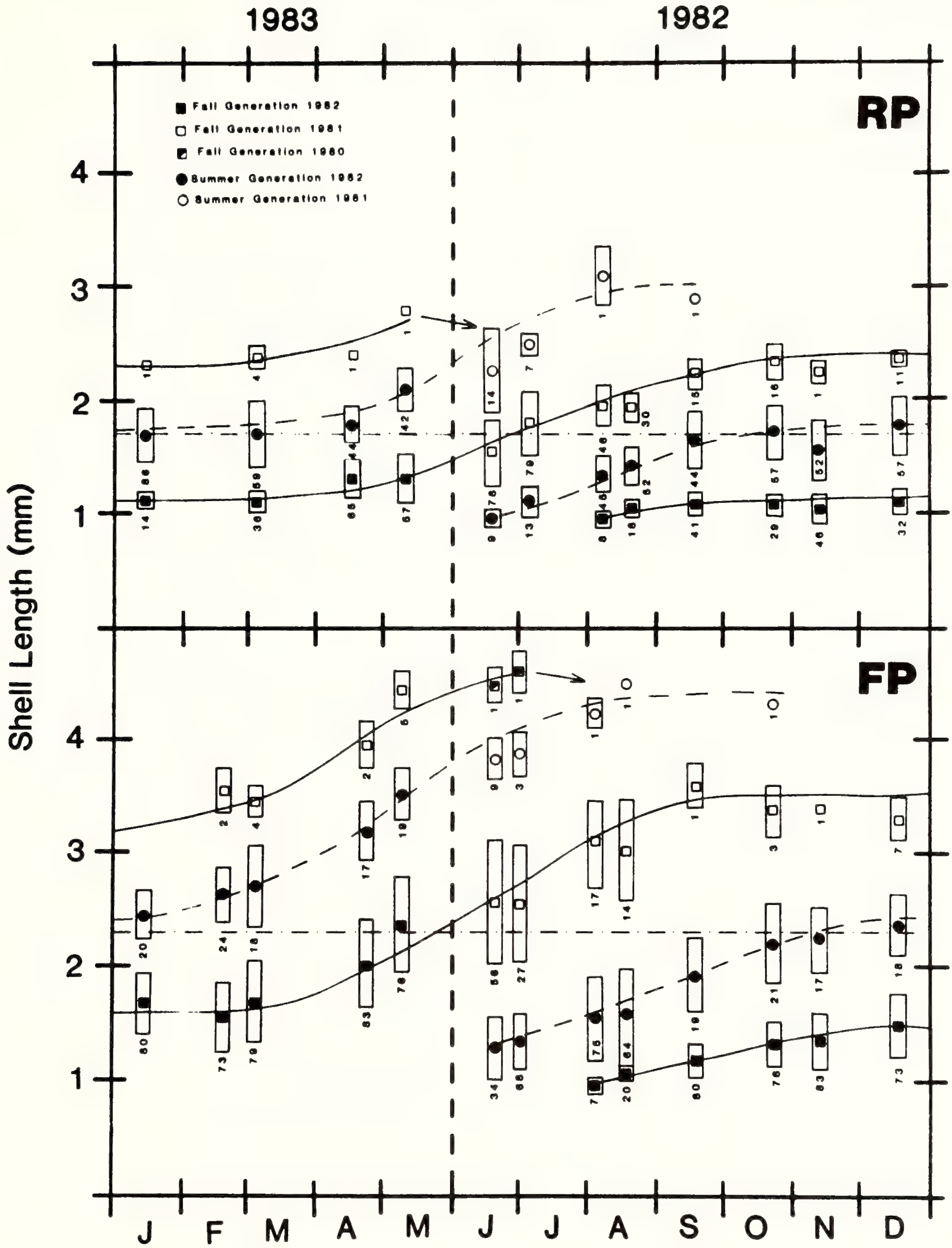

Fig. 3. Changes in mean shell lengths for various generations of *Pisidium casertanum* for the period June 1982 - May 1983 from two ponds in southwest Virginia (Riopel Pond - RP and Farriers Pond - FP). Boxes around means are standard deviations. The horizontal dash-dot lines indicate the minimum size needed to produce young (1.7 mm from RP and 2.3 mm from FP). Numbers below means are the percentages of the total population that the specific generation constitutes. Data for January - May 1983 were plotted before the June - December 1982 data to facilitate the observation of annual trends. This assumed little year to year variation in population dynamics.

Table 2. Univariate analyses of variance of the effect of pond of origin, month of year (MO) and adult shell length (SL) on the number of embryos 0.1 mm (size 1), 0.2-0.6 mm (size 2) or > 0.7 mm (size 3) in length.

	Embryo Size 1		Embryo Size 2		Embryo Size 3	
Factor	df	Sum of Squares	df	Sum of Squares	df	Sum of Squares
Pond	1	251.6**	1	707.2**	1	3.5
Month	11	4169.6**	11	1659.4**	11	40.1
SL	1	123.2*	1	415.9**	1	16.9
Pond x MO	9	53.9	9	1296.6**	9	32.6
Pond x SL	1	2.7	1	54.1	1	1.9
SL x MO	11	746.8**	11	552.3**	11	58.9
Pond x SL x MO	9	41.7	9	71.3	9	8.6

* significant at the 0.05 level

** significant at the 0.01 level

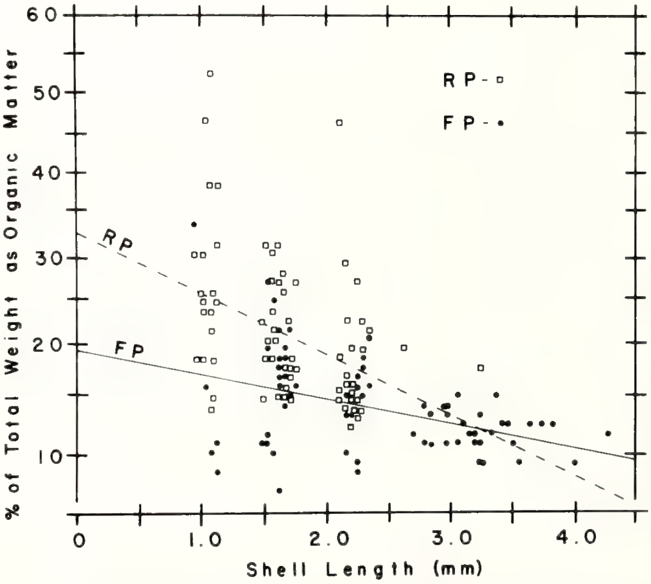

Fig. 4. Relationship between size (as shell length) and the percent of total weight as organic matter for two populations of *Pisidium casertanum* from southwest Virginia (RP = Riopel Pond; FP = Farriers Pond). Lines are based on linear regressions of shell length on the arcsine transformation of % of total weight as organic matter.

those transferred from the harsher of the two ponds (RP) to the more favorable environment (FP) flourish, while those clams in the reciprocal transfer from favorable to harsh (i.e. FP→RP) do not fair well. This can be due to the poorer ion availability in RP compared to FP or other factors such as lowered food availability and cooler temperatures.

In addition to differences displayed in survivorship patterns, there were differences in reproductive output from clams in the various transfers. Table 4 gives the birth rates of various sizes of adults over two time periods during the transfer: July and August. Two-way analyses of variance on the affect of age and transfer on birth rates for the two periods indicated that there were significant age and transfer effects on birth rates for both periods (transfer effect: F = 4.00 3,78 df, prob. F = 0.011, and F = 2.79 3,77 df, prob. F = 0.047 for July and August respectively; age effect: F = 14.31 3,78 df, prob. F = 0.0001, and F = 8.34 3,77 df, prob. F = 0.0001 for July and August respectively) but there was no significant interaction effect between age and transfer on birth rate (F = 1.34 5,78 df, prob. F = 0.26 and F = 0.68 5,77 df, prob. F = 0.64 for July and August respectively). In general, birth rates are greatest for adults in the FP control group (FP→FP transfer) or in the FP→RP transfer and lowest in the RP control group. It is interesting to note that clams from RP transfered to FP, a more favorable habitat, have increased birth rates. Whether this represents increased fecundity or increased survivorship of embryos is not known. It is probable, however, that an increased survivorship of embryos is a more likely explanation since most of the young being born during July and August began their development in late June or early July, before the onset of these transfer experiments (see Fig. 2).

LABORATORY EXPERIMENTS

Experiments culturing clams in water of various hardness were conducted from late June 1982 through January 1985. In these experiments there was an effect of water hardness on growth, survivorship and fecundity of clams. In addition, there was an effect of pond of origin (FP vs. RP) on these life history traits.

Typically, within a run of clams from either FP or RP, individuals maintained in pond water grew to a larger size than clams maintained in other treatments (Fig. 6). Growth rates varied in other treatments dependant on pond of origin. For example, poorest growth was observed in very hard and hard water for individuals from FP and RP, respectively. There appears to be no clear cut influence of water hardness on growth rates based on these experiments since it would be expected that clams from RP grown in water with greater ion content than pond water should have increased growth rates. Also, none of the clams from FP reached shell lengths characteristic of their natural habitat (i.e. FP clams often reach sizes > 3.0 mm but none reached this size in these experiments). There is, however, an effect of pond of origin on how clams grew in the water of various hardness (Fig. 7). Based on t-tests conducted for each date for each treatment (i.e. water hardness), the following results were found. In pond water, clams from FP generally had larger mean shell lengths from the beginning of the experiments until July 1983 (approximately day 350) at which time there was no significant difference in mean shell length until the clams from RP died. In very soft water, clams from RP had significantly larger mean shell lengths from the beginning of the experiments until February 1983 (approximately day 270). Following this date there were no significant differences. In soft water, again clams from RP had significantly larger mean shell lengths until July 1983 (day 350) and then there was no difference. In hard water there was no significant difference in shell length until September 1982 (approximately day 80) and then clams from FP had significantly greater mean shell lengths than clams from RP. There was no significant difference in shell lengths of clams maintained in very hard water at any time. These results, again are difficult to interpret and show no clear pattern of water hardness effect on growth except that in softer waters clams from RP appeared to grow slightly better than clams from FP but in hard water clams from FP seemed to grow better. Part of the inconsistency in pattern has to do with differences in survivorship patterns under various treatments. Since clams die at different rates in these treatments (see below) this affects mean shell lengths differentially. It might have been better to isolate individual clams and follow individual growth rates rather than mean

Table 3. Survivorship data, partioned by treatment, for various sizes of *Pisidium casertanum* from transfer experiments between Riopel Pond (RP) and Farriers Pond (FP). The numbers in parentheses after the median survival times are standard errors.

TREATMENT Pond of Origin → Pond of Transfer	Initial Size (mm)	Median Survival Time (Days)	Number of Individuals at start of Experiment
FP → FP	NB*	65.1 (2.2)	172
	≤ 1.2	75.7 (1.7)	30
	1.3 - 2.0	79.7 (1.5)	40
	2.1 - 2.5	83.5 (2.8)	27
	> 2.5	113.3 (2.4)	40
FP → RP	≤ 1.2	7.8 (1.2)	40
	NB*	37.6 (1.0)	131
	1.3 - 2.0	46.7 (3.0)	40
	> 2.5	49.9 (1.3)	40
	2.1 - 2.5	50.4 (2.9)	40
RP → RP	≤ 1.2	24.2 (2.1)	60
	NB*	40.6 (4.6)	11
	2.1 - 2.5	83.4 (4.9)	50
	1.3 - 2.0	90.9 (9.6)	60
	> 2.5	122.5 (4.3)	6
RP → FP	NB*	51.4 (3.3)	45
	≤ 1.2	70.0 (6.3)	40
	2.1 - 2.5	76.0 (3.7)	40
	1.3 - 2.0	118.4 (4.0)	40
	> 2.5	(—)	0

*newborns - clams born during the transfer of experiments

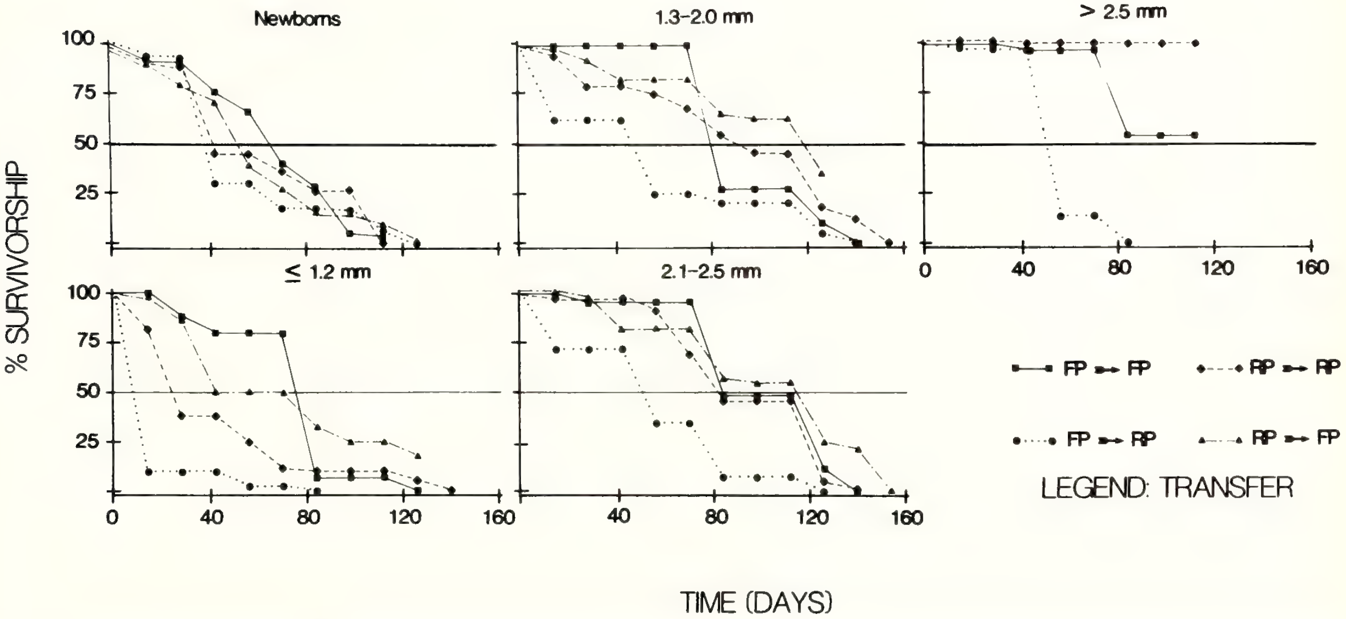

Fig. 5. Survivorship curves for 5 size categories of *Pisidium casertanum* involved in transfer experiments between two ponds in southwest Virginia (RP = Riopel Pond; FP = Farriers Pond).

Table 4. Birth rates (number of young/adult/week) for *Pisidium casertanum* utilized in transfer experiments between Riopel Pond (RP) and Farriers Pond (FP). Rates are averages for the months of July and August 1982. Numbers in parentheses are standard deviations.

JULY

Adult Shell Length (mm)	Pond of Origin → Pond of Transfer			
	FP → FP	FP → RP	RP → RP	RP → FP
≤ 1.2	0	0	0	0
1.3 - 2.0	0.018 (0.049)	0 —	0.012 (0.033)	0.057 (0.083)
2.1 - 2.5	0.176 (0.315)	0.209 (0.263)	0.023 (0.042)	0.266 (0.271)
> 2.5	0.830 (0.850)	1.093 (0.863)	0 —	0.280 (—)

AUGUST

Adult Shell Length (mm)	Pond of Origin → Pond of Transfer			
	FP → FP	FP → RP	RP → RP	RP → FP
≤ 1.2	0	0	0	0
1.3 - 2.0	0 —	0 —	0.005 (0.013)	0.031 (0.063)
2.1 - 2.5	0.152 (0.198)	0.019 (0.041)	0.027 (0.047)	0.023 (0.045)
> 2.5	0.373 (0.399)	0.211 (0.312)	0.094 (—)	0.304 (—)

growth rates.

In terms of survivorship, within a run, clams maintained in pond water generally had better survivorship than clams in other treatments (Table 5 and Fig. 8). The next best survivorship was seen in hard water followed by very hard and/or soft water with the poorest survivorship in very soft water. Consequently it is possible to say that water hardness does have a significant effect on survivorship, but again there is no direct correlation of survivorship with increased ion content since clams maintained in pond water from RP had higher survivorship than clams from RP maintained in water of higher ion content. It is interesting to note, however, that in the artificial waters (non-pond water treatments) clams maintained in hard water had the best survivorship. Clams maintained in very hard water were observed to have a very dark brown color and what appeared to be precipitates on their shells. Thus, too many ions in the water seemed to adversely affect survivorship. In all cases, clams from FP had better survivorship than clams from RP (Table 5).

ELECTROPHORESIS

The preliminary results of an electrophoretic analysis of these two populations of *Pisidium casertanum* is given in Table 6. In addition to the 4 enzyme systems noted in this table, attempts were made at resolving 7 other enzyme systems (ADH, CAT, GOT, IDH, LAP, MDH and ME). The majority of these systems showed poor resolution and/or poor mobility. However, the LAP and IDH banding patterns were quite complex and not easily scored. The IDH system showed a five-banded pattern in some individuals and a three-banded pattern in others. The LAP system also showed a complex three-banded pattern. Due to the complexity of these systems, which could be due to gene duplications or the possible existence of polyploidy in the genus *Pisidium* (see Burch, 1975:viii), these systems were not included in the estimation of the genetic relatedness of these populations. The average genetic distance between these two populations of *P. casertanum* is 0.147. It should be noted that all of the clams from RP displayed the same genotype while those from FP displayed a range of genotypes including the RP genotype.

DISCUSSION

This study presents data on the life history characteristics of two populations of *Pisidium casertanum*. A summary of the life history characteristics of other populations of this species can be found in Table 7. In these studies, life spans of from < 1 to 5 years as well as great variations in reproductive output have been described for the species. Despite this fact little experimental work has been conducted to examine the casual force in the noted differences. The population from RP has the smallest maximum shell length of any population examined to date. This is probably not due to low temperatures experienced at high altitude (the creek population studied by Burky *et al.*, 1981 never experienced temperatures > 15ºC) nor food availability (the population

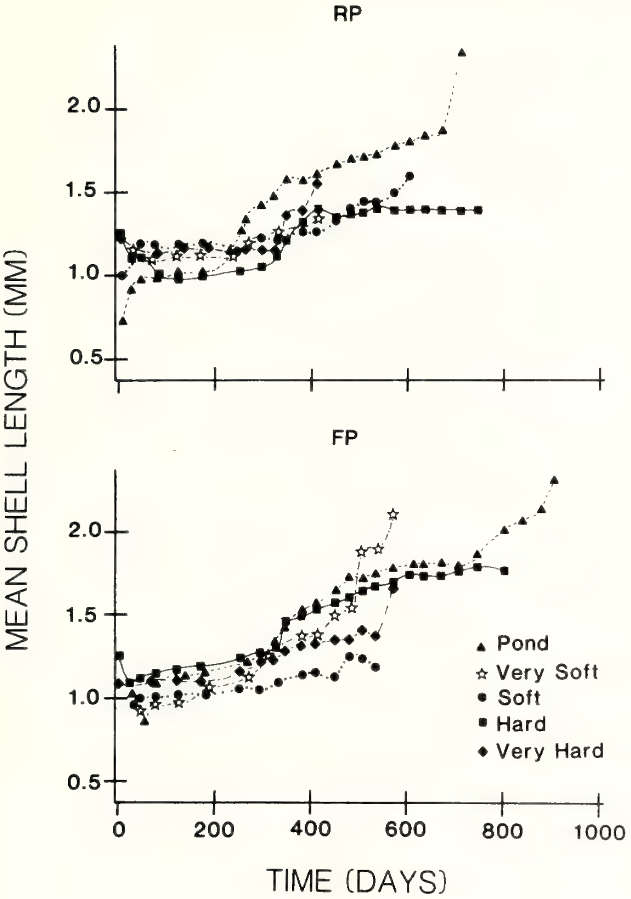

Fig. 6. Growth curves (as increases in mean shell length) for *Pisidium casertanum* taken from two ponds (RP = Riopel Pond; FP = Farriers Pond) and reared in waters of various hardnesses.

studied by Holopainen, 1979 was from an oligotrophic lake). The differences may, however, be due to calcium availability or low alkalinity. Potentially calcium availability could affect both size and composition. Of those populations of *P. casertanum* shown in Table 7 for which water chemistry data were available, RP certainly had the lowest calcium availability, conductivity and alkalinity (Table 1). The low alkalinity and calcium levels may inhibit shell formation in this population. Figure 4 emphasizes the fact that clams of equivalent shell lengths have much less $CaCO_3$ if they are from RP as compared to clams from FP.

The data in Table 7 provide a preliminary data base for analyzing the relationships among various life history traits in *Pisidium casertanum*. Stearns (1976) has suggested that based on certain theories of life history evolution (r and K and bet-hedging theories) that suites of life history traits should covary giving rise to "life history tactics". Whether or not strict covariation is needed in observing life history tactics is a matter of some debate (see e.g. Stearns 1980, 1982; Etges, 1982; Wittenberger, 1981). Also all one-dimensional models of life history evolution assume equilibrium population sizes (Caswell, 1983) which probably rarely occurs in the Pisidiidae. Brown (1985a) and Way (1985) claim that more examples of intraspecific variations in life history traits are needed to examine life history evolutionary models. A principal components analysis (SAS Institute, 1982) was conducted using the data in Table 7. The life history traits used in this analysis included maximum shell length, maximum life span, number of generations produced per year, age at first reproduction and maximum number of embryos per parent. Utilizing these traits allowed 7 of the 10 populations to be included in the analysis.

The first two principal components accounted for 70% of the variation in the life history traits. The variables age at first reproduction, number of generations per year and maximum shell length loaded most heavily for the first principal component. The variables maximum life span and maximum shell length loaded most heavily for the second principal component.

A plot of the principal component scores based on the first two principal components is shown in figure 9. The first principal component is a composite of increasing age at first reproduction and maximum shell length and decreasing number of generations produced per year. Populations to the right of the vertical line drawn in figure 9 display one generation per year while those to the left display two. The second principal component is a composite of increasing maximum life span and decreasing maximum shell length. One could interpret those populations shown above the horizontal line drawn in figure 9 as being from more stable habitats (ponds and lakes) whereas those below the line are from more variable habitats (temporary ponds and streams).

Associated with the increased predictability of the habitat (populations above the horizontal line) is increasing maximum life span and to a lesser extent (lower loading value for the second principal component) decreasing maximum shell lengths. Within the permanent habitats (above the horizontal line) RP is certainly the harshest habitat (low temperature, oligotrophic and has low calcium availability and alkalinity). The populations to the right on this graph are from more favorable permanent habitats (ponds and lakes with at least higher calcium availability). This trend of increasing favorableness of the habitat with an increase in the first principal component is also seen within the more variable habitats with streams being found to the right of a temporary pond in figure 9. This increase in favorableness of the habitat, whether in a stable or variable habitat, is associated with a switch from producing two generations per year to producing only one generation per year and an increase in maximum shell length attained.

The two dimensional nature of the results of this principal component analysis is similar to Greenslade's (1983) habitat template. In Greenslade's model, two axes to be dealt with when considering life history evolutionary "strategies" are habitat favorableness and habitat predictability. The third axis in the habitat template deals with biotic predictability and is a function of the other two axes. Thus, in predictable yet harsh habitats (e.g. RP) one finds reduced reproductive output, long life span and small total size. These are traits associated with adversity selection and are expected based

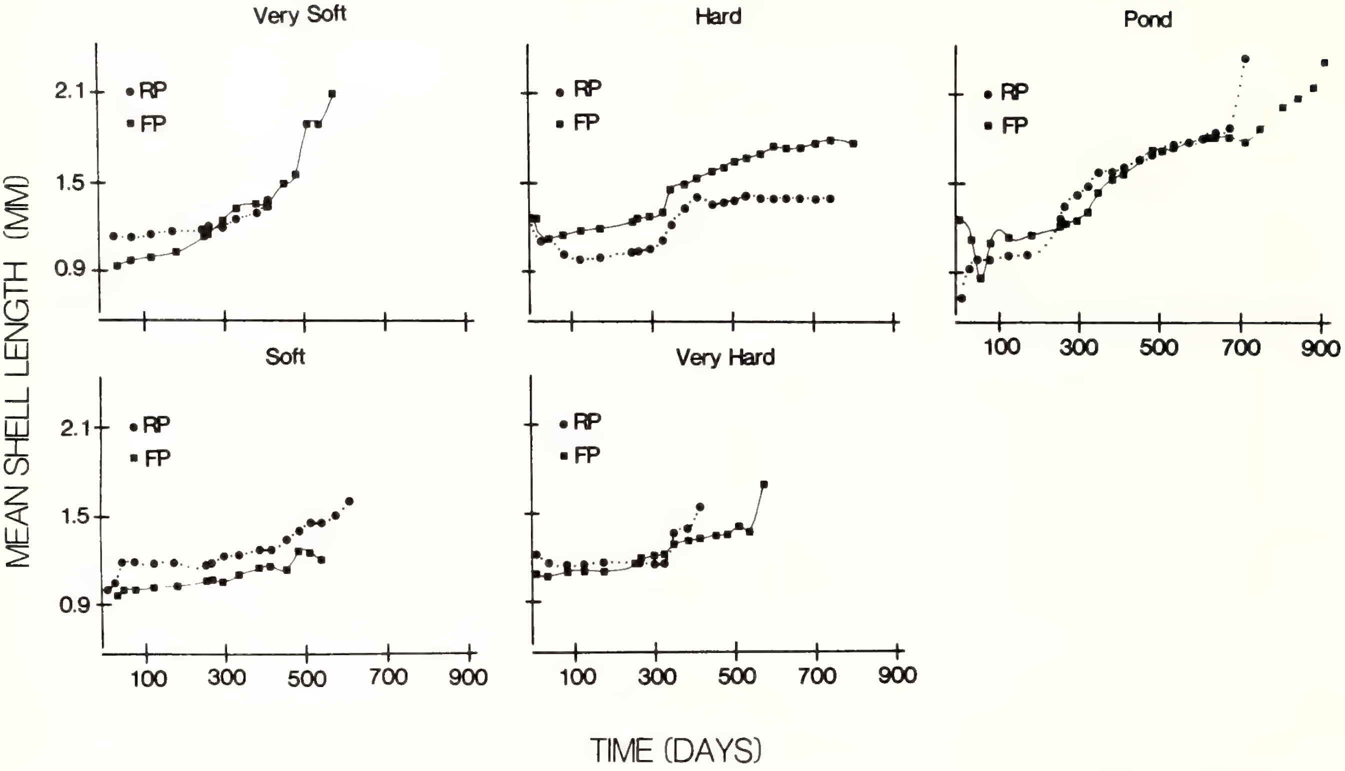

Fig. 7. Growth curves (as increases in mean shell length) of *Pisidium casertanum* reared under various water hardnesses. Clams were taken from either Riopel Pond (RP) or Farriers Pond (FP).

on Greenslade's model. In a predictable and favorable habitat (e.g. a lake) one finds long life span, an increased maximum shell length, an increased age at first reproduction and the production of only one brood per year. These traits are associated with "K-selection" and again are expected based on Greenslade's model. One important point of the principal component analysis is that strict covariation of life history traits is not found. Variable and stable habitats which are both favorable (e.g. a stream and a lake) may display similar ages at first reproduction, number of generations produced per year and maximum shell lengths attained (at least not separable based on principal component analysis) but they do differ considerably in life span (Fig. 9, Table 7).

In addition to the variation in life history traits noted above, there are differences in physiological traits in these two populations. Hornbach (1985) has shown that metabolic rates of clams from FP may be as much as 11 times higher than for individuals from RP at comparable temperatures. The lowered overall metabolic rate of clams from RP can lead to a lowered amount of ingestion and assimilation and could result in the smaller shell lengths (Figs. 1 and 3) and reduced reproductive output (Fig. 2, Tables 2 and 4) noted for this population, again attesting to the harsh environmental conditions in RP.

The question of interest is how much of the variation in life history traits that is noted interspecifically is due to genotypic differences in populations and how much of the variation is totally environmentally induced. Brown (1985a) has found that much of the intraspecific variability in populations of pulmonate snails is environmentally induced and Russell-Hunter (1978) claims that much of the variation in life histories in freshwater snails is also due to phenotypic plasticity. Little work has been conducted on the importance of environment vs. genotype in life history variation in freshwater clams. The data presented here provide some insight to these questions.

The transfer experiments show that there are both environmental influences on the expression of particular life history traits and potentially some genetic influences. For example, the increased reproductive output by individuals from RP transferred to FP (Table 4) shows an environmental effect, but the fact that the reproductive output does not reach the levels of those clams from FP indicate that the pond of origin (or differential genotype or developmental history) can also influence this life history trait. It is also possible, however, that the increase in reproductive output was only due to increased embryonic survivorship and that the transfer experiments were too short to allow for the assessment of changes in fertility which could allow clams from FP to rival the fecundity of individuals from FP. If, however, the birth rates of transfers are representative of true phenotypic shifts and the differences in birth rates noted for clams in their home ponds has a genetic component, then the changes in birth rate noted may be an example of cogradient selection where the

Table 5. Median survival times for *Pisidium casertanum* of shell lengths ≤ 1.2 mm from either Riopel Pond (RP) or Farriers Pond (FP) maintained under conditions of varying water hardness. Numbers in parentheses are standard errors.

	RP		FP	
Water Hardness	Number of Individuals at start of Experiment	Median Survival Time (days)	Number of Individuals at start of Experiment	Median Survival Time (days)
Very Soft	23	136.5 (34.1)	75	213.8 (10.8)
Soft	39	45.7 (21.6)	108	227.7 (13.5)
Hard	35	293.6 (39.1)	84	397.9 (31.5)
Very Hard	17	217.5 (30.9)	70	257.5 (12.4)
Pond*	31	542.9 (23.2)	137	615.0 (175.6)

* - a control series that consisted of water from the pond of origin, i.e. pond water for clams from RP was water from RP and pond water for clams from FP was water from FP.

Table 6. Allele frequency for 10 presumptive loci for 4 enzyme systems of *Pisidium casertanum* from Farriers Pond (FP) and Riopel Pond (RP). Nei's identity (I) was calculated from the frequency data. N is the number of individuals analyzed. Abbreviations follow Hornbach *et al.* (1980a) and Werth (1985).

Enzyme System	Locus	Population	Allele Frequency			I	N
			a	b	c		
PEP	1	FP	0.75	0.25	—	0.949	20
		RP	1.00	0	—		20
	2	FP	1.00	0	—	1.000	20
		RP	1.00	0	—		20
	3	FP	0.45	0.50	0.05	0.741	20
		RP	0	1.00	—		20
PGI	1	FP	0.25	0.75	—	0.316	20
		RP	1.00	0	—		20
	2	FP	1.00	0	—	1.000	20
		RP	1.00	0	—		20
EST	1	FP	1.00	0.00	—	1.000	27
		RP	1.00	0.00	—		29
	2	FP	1.00	0.00	—	1.000	27
		RP	1.00	0.00	—		29
	3	FP	0.44	0.55	—	0.625	27
		RP	1.00	0.00	—		29
PGM	1	FP	1.00	0.00	—	1.000	7
		RP	1.00	0.00	—		9
	2	FP	1.00	0.00	—	1.000	7
		RP	1.00	0.00	—		9

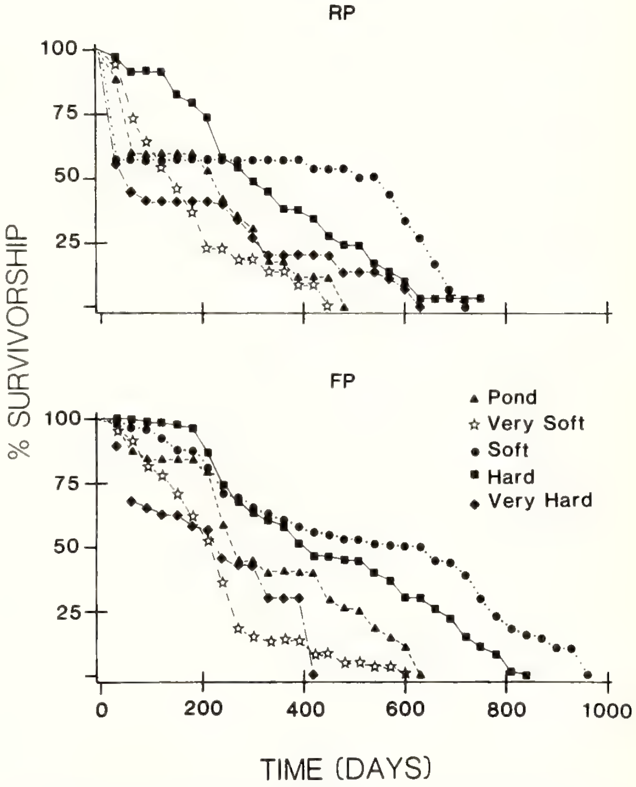

Fig. 8. Survivorship curves for *Pisidium casertanum* taken from two ponds (RP = Riopel Pond; FP = Farriers Pond) and reared in waters of various hardnesses.

genotypic variation is consistent with the observed phenotypic variation (Berven *et al.*, 1979). The transfer experiments were too short to allow for the examination of environmental influences on growth although variations in survivorship patterns did appear to have an environmental component since clams transferred from FP to RP had a decrease in survivorship while those transferred from RP to FP generally had an increased survivorship (Table 3), especially when considering smaller (younger) clams. Since young clams from RP transferred to FP have survivorship rates less than those from FP and since those transferred from FP to RP also have lower survivorship than those from RP this could be a case of maximizing selection (Berven *et al.*, 1979) where the phenotype is maximized in all cases. The data on survivorship and growth, however, are merely suggestive in this area and not conclusive.

Despite the fact that environment seems to play a role in accounting for differences in life histories displayed by

Table 7. Life history traits of 10 populations of *Pisidium casertanum*.

Maximum Shell Length (mm)	Maximum life span (mo)	Number of generations per year	Major Birth Periods	Minimum Age at first Reproduction (mo)	Maximum Number of embryos per parent	Maximum Embryo Size (mm)	Habitat	Reference
4.2	36	1	July	10	27	1.0	Lake (Littoral)	Holopainen, 1979
4.3	60	1*	April, Dec*	24	20	1.1	Lake (Profundal)	Holopainen and Jónasson, 1983
4.0**	?	?	June-August**	?	17	1.25	Lake (Littoral)	Odhner, 1929
3.6	?	2(?)	Feb, August (?)	?	25	1.2	Lake (Profundal)	Thut, 1969
5.0	12	1	July	24	8	1.5	Temporary creek pool	Mackie, 1979
4.2	10	2	June, Aug-Oct	4	8	1.5	Temporary pond	Mackie, 1979
4.8	12	1	May-July	24	32	?	Creek	Heard, 1965
4.8	24	1	April-Aug	24	?	?	Creek	Burky *et al.* 1981
4.8	24	2	June, Aug-Oct	10	33	1.3	Pond (FP)	This study
3.3	20	2	June, Aug-Oct	4	16	1.0	Pond (RP)	This study

* dependent on time of lake turnover
**at least — full data not available

these two populations of clams, there are genetic differences in the populations. Starch gel electrophoresis (Table 6) indicates that all of the individuals from RP are of the same genotype while a number of genotypes (including the RP genotype) can be found in the FP population. The genetic distance between these two populations (0.147) is quite high and is higher than that reported for intraspecific distances in other pisidiid clams (e.g. *Sphaerium striatinum* (Lamarck), Hornbach *et al.*, 1980a). Consequently it is possible to state that there is a genetic difference between the two populations or at least a difference in the expression of genotype. Whether the variation in enzyme pattern noted results in differences in life histories is unknown.

Results of the electrophoresis indicate that there is a genetic difference between the two populations but the transfer experiments also indicate the importance of environmental factors. An obvious candidate for the causal environmental agent is calcium availability or alkalinity (RP has much lower levels of both than FP, see Table 1). It has been noted that calcium availability and alkalinity are important components in the deposition of molluscan shells (Wilbur, 1964). Mackie and Flippance (1983a, b) and Burky *et al.* (1979) have shown that calcium availability and trophic status can be important factors influencing shell composition in the pisidiids. Figure 4 shows that clams from FP, where calcium content and total alkalinity is high, have a greater percentage of their weight as $CaCO_3$. It is possible then that ion availability is influencing the physiology of shell deposition in these clams. Whether or not ion availability is also capable of influencing life history traits is still unclear, even after the laboratory experiments conducted here.

In the laboratory experiments, clams did not grow to their normal maximum size, and only a few individuals from FP maintained in pond water were able to reproduce. The reasons for this poor performance is unknown, although maintaining the clams at constant temperatures and light could have influenced the normal seasonality of their reproduction, and feeding them artificial food could have reduced their growth rates. Mackie and Qadri (1978) has indicated that *Musculium securis* (Prime) requires a substratum for growth although *M. partumenium* (Say) has been cultured with artificial food for 3 generations (Childers and Hornbach, 1983 and personal observations). Regardless of the poor performance, laboratory experiments do show that calcium availability (or at least ion availability) does influence growth and survivorship.

Again the laboratory experiments give an indication that not only are environmental factors important in influencing life history traits but pond of origin (genotype or developmental history) may also have an influence. Differences in growth and survivorship were noted in some cases between populations subjected to the same water hardness (see Results). It is possible that in very soft and soft waters clams from RP had better growth on the average than clams from FP (Fig. 7) because they are from a pond low in ion content. However, over time, those clams from FP which cannot survive low ion availability died and those that survived (possibly of the same genotype as those from RP?) were able to display similar rates of growth as those from RP. Clams maintained in pond water from either FP or RP did equally well possibly because they were being maintained in water in which they developed. It is still unclear as to why clams from FP did not reach a shell length characteristic of their home pond. Possibly there were cage effects. They were able to reproduce, however, clams from RP never did in the laboratory experiments. This suggests that the conditions under which these clams were maintained were not ideal for examination of growth and reproduction but they did quite well in survivorship.

This work shows there are intraspecific variations in life histories displayed by *Pisidium casertanum*. The differences probably have both genetic and environmentally in-

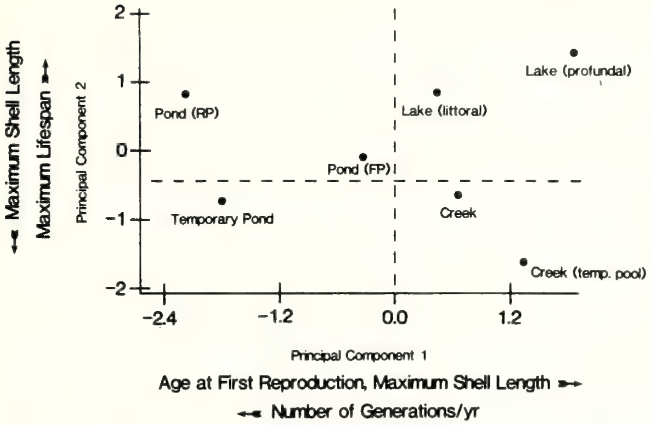

Fig. 9. Graph of the principal component scores, based on the first two principal components, for life history traits of 7 populations of *Pisidium casertanum.* The data for this analysis are found in Table 7. Increasing age at first reproduction and maximum shell length and decreasing number of generations per year were the factors that loaded most heavily for the first principal component. Increasing maximum life span and decreasing maximum shell length were the factors that loaded most heavily for the second principal component. Dashed lines are used in discussion of the role of habitat predictability and habitat favorableness in influencing life history trait suites (populations above the horizontal are considered predictable compared to those below the horizontal while populations to the left of the vertical are considered unfavorable compared to those to the right).

duced components. Factors such as habitat stability and habitat favorability appear to be quite important in structuring the suites of life history traits displayed. Improved methods for quantifying the variations in life history traits are needed so that an estimate of the importance of genotype versus environment in accounting for the great deal of phenotypic plasticity found in freshwater molluscs (Russell-Hunter, 1978; Burky, 1983) can be made. In addition, more work on intraspecific variations in life histories is needed to examine proximate causes of their evolutionary change. *P. casertanum* can be a good candidate because of its worldwide distribution, its great abundance and because of great variations in life histories.

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EFFECTS OF WATER FLOW ON THE DETACHMENT OF SOME AQUATIC PULMONATE GASTROPODS

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ABSTRACT

Detachment behaviour of several taxa of aquatic pulmonate molluscs was studied in a tubed, flowing water system. The species investigated were *Lymnaea peregra* (Müller), *L. stagnalis* (L.), *Planorbis planorbis* (L.), *P. vortex* (L.), *Bulinus jousseaumei* (Dautzenberg), *Biomphalaria glabrata* (Say) and *Physa fontinalis* (L.). The discharge of water encountered by the snail before detachment was measured in relation to several factors, which included shell profile exposed to the current, body mass and foot area. Using analysis of variance and multiple regression techniques, profile was found to be the predictive variable for most of the species tested. There were negatively sloped linear relationships between profile and detachment time. Planispiral shaped snails such as *Biomphalaria* and *Planorbis* had the most direct relationships. The more globose snails such as *Bulinus* and *Lymnaea* had much less predictable responses. There were interspecific differences between snails in their detachment times, and for *L. peregra* at least, time of year and feeding regime were also important variables.

Aquatic gastropods can be vectors of a number of helminth infections including schistosomiasis and fascioliasis. The introduction of irrigation channels from areas in which there is a degree of infection into areas where there is little degree of infection can seriously increase infection rates in local host populations. For some time, engineers have been aware of these risks and have attempted to take these factors into account in channel design (Araoz, 1962). Research in which snails are exposed to different velocities of water flow in experimental channels has helped to determine many of the design criteria. For example, Jobin and Ippen (1964) investigated the behaviour of *Biomphalaria glabrata* (Say) in open channels. Firstly, empty shells, tethered to a Newton meter, were used to measure drag forces and secondly, measurements of absolute snail strength were made, thereby leading to the prediction that the snails would probably dislodge at a flow rate of 0.94 $m \cdot s^{-1}$. When live snails were tested in flowing water, the prediction came close to being fulfilled, with snails dislodging at 0.65 $m \cdot s^{-1}$.

Although Jobin and Ippen (1964) measured the maximum velocity at which snails could retain their grip, little measurable correlation was found between snail size and ability to stay attached. It was necessary to make sensible use of envelope curves to graphically represent the relationships between (a) water velocity at which detachment occurred and (b) the diameter of the ramshorn, or planispiral, shaped shells. A similar pattern of results for *Biomphalaria pfeifferi* (Krauss) was obtained by Madelin (1984) although detachment velocities were lower at 0.33 $m \cdot s^{-1}$.

Experiments have also been done on other, non-vector species including *Stagnicola palustris* (Müller) and *Physa propinqua* (Tryon) (Moore, 1964). This research involved the use of snails in open channels but in a multivariate experimental design. The number of snails detaching at different velocities on a variety of substrata were measured, and it was possible to show a curvilinear relationship of detachment velocity with snail shell length; substratum type appeared to be a highly significant variable. Flow rates were measured with a mechanical, propellor driven, flow meter.

These works did not take particular account of the fatiguing effect of continuous exposure to a flow of water. Dorier and Vaillant (1948) did take this factor into account to a limited extent in their studies on a variety of invertebrate species including *Theodoxia fluviatilis* (L.), *Ankylastrum fluviatile* (Müller), *A. capuloides* (Jan.), *Radix limosa* (L.), *Physa fontinalis* (L.), *Bythinia tentaculata* (L.) and *Lymnaea stagnalis* (L.). A Pitot tube was used to measure local water velocity at depths as low as 3mm from the substratum. *R. limosa* and *L. stagnalis* detached at flow rates of 0.202 and 0.75 $m \cdot s^{-1}$ respectively but snail structural dimensions were not taken into account.

The aims of the present work were therefore, (1) to devise an apparatus in which aspects of snail detachment behaviour could be investigated, (2) to identify dimensional aspects of snail hydrodynamics which might be related to detachment and (3) to compare the detachment performance of a range of species, including some schistosomiasis vectors. The species investigated were an albino and a pigmented

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form of the schistosome vector *Biomphalaria glabrata; Bulinus jousseaumei* (Dautzenberg) which is also a schistosome vector; *Lymnaea peregra* (Müller) which can be a liverfluke vector; *Physa fontinalis* (L.), a snail commonly found in pond weed; *Lymnaea stagnalis* (L.), *Planorbis planorbis* (L.) and *P. vortex* (L.) which are all still-water snails. The first two species are tropical and the remainder are wild snails in the United Kingdom.

MATERIALS AND METHODS

The previously described experiments used square sectioned open channels. I used similar channels in preliminary trials but felt that the corners and broken water surface presented an unnecessarily complicating factor at this stage of the work. The effect of flow in a round sectioned tube was therefore investigated.

The apparatus design is given in figure 1. An Otter water pump with a maximum capacity of 0.5 $dm \cdot s^{-1}$ was used to deliver water to an upper reservoir of 15 dm^3 capacity, 0.57 m above a similar sized lower reservoir. Suitable overflows were used to maintain a constant head of water, which was delivered to the test chamber through a calibrated gate valve. The discharge rate at each valve opening was empirically obtained by measuring the time taken to discharge 10 dm^3 to an empty chamber; this converts to an average flow rate of 0.86 $m \cdot s^{-1}$ at maximum discharge.

The tubing and test chamber were made of transparent poly-vinyl chloride (PVC) tubing (internal diameter 0.025 m) connected by push fittings. Snails could be easily introduced to the test chamber by closing the gate valve, emptying the lower chamber and introducing the snail into the empty test chamber which had previously been wetted. The snails, which were tested singly, usually attached within 30 seconds. By lowering the upstream end of the test chamber, and by slowly opening the gate valve, snails could be fully immersed without encountering turbulence. The lower reservoir was then filled, the test chamber made horizontal and the pump started. The gate valve was opened one stop per 10 seconds, thereby exposing the snail to a known discharge.

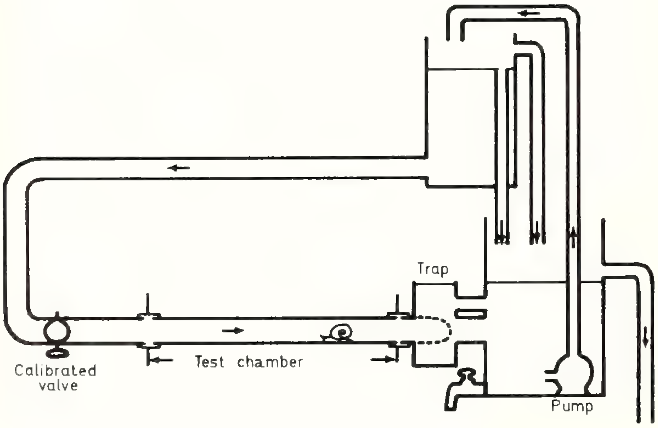

Fig. 1. Design of the apparatus.

At maximum velocity, the length of time until the snail detached was recorded. Since the discharge at maximum flow was known, the total discharge as $m^3 \cdot s$ encountered by the snail from the start of the experiment up to detachment could be calculated. Similarly, approximate velocities of flow in the pipe could be calculated, though this was not the prime intention. Data on velocity are, however, useful for comparison with results of other authors. A capillary bore manometer was used to measure the local relative flow rate at intervals of 2 mm from the wall of the tube to its centre.

A video camera system was used to visualise the flow in the test chamber. Black particles of Zeocarb, which has a slightly negative buoyancy, were fed into the system. Freeze frame photographs were taken of the video screen and it was possible to follow the paths of particles in tubes with and without snails present.

As well as the detachment time for each snail tested in the apparatus, a number of other parameters were measured. Mass was obtained by weighing a live snail from which excess water had been blotted. Area of the foot when fully extended was measured by allowing the snail to crawl on a plastic petri-dish. A stylus could then be used to scratch the outline of the foot from underneath. This outline was placed over a piece of mm graph paper and squares counted. The area of the smallest profile was obtained by placing the snail in the light path from a distant light source and tracing the outline of the shell on graph paper before counting squares. The area of the largest profile was obtained in a similar way, but this aspect was not found to be significant in the analysis and these data were ignored.

The absolute strengths of a number of snails were measured. Jobin and Ippen (1964) obtained their results by putting a small harness on the snail under investigation; they then used gramme masses to cause the snail to detach. It is difficult to treat such data as a continuous variable and I therefore allowed a snail to become mobile in water in a dish on the top of an Oertling top pan balance. The force that the snail exerted to maintain its grip while being gently lifted off was then measured. The balance gave an output to a chart recorder; this meant that the application of a firm continuous pull could be verified. Various mechanical devices including pulleys and harnesses were tried, but the most effective and reliable method of removing the snails was to first gently tease and then lift the snail by forceps.

RESULTS

Reynold's number (R) for a flowing water system is a dimensionless value that can indicate whether flow is smoothly laminar or turbulent (Cartwright, 1985). The number is given by

$$R = \frac{\varrho \, v \, d}{n}$$

where ϱ = density of liquid $kg \cdot m^{-3}$ (1000 for water), v = velocity $m \cdot s^{-1}$ (0.860 for this system), d = diameter of tube (0.025 m), and n = viscosity of water (0.0013 $N \cdot s \cdot m^{-2}$).

In natural waters, stream flow is almost always turbulent (Hynes, 1970). In my experiments, $R = 16{,}538$ at maximum velocity, which is just about the turbulent flow threshold value of $R =$ within 1100-50,000. When the test chamber was empty of snails, the video recording showed a slight sinuous tracking of particles. When snails were present, turbulent eddies (Karman street vortices) were visible downstream of the snail (Fig. 2). Local flow rate measurements, obtained by use of a capillary manometer showed a velocity profile transitional between those characteristic of laminar and turbulent flow (Fig. 3).

The drag coefficient (cd) for a snail is given by the equation

$$cd = \frac{2f}{a \cdot \varrho \cdot v^2}$$

where f = resistive force, a = area exposed to the flow, ϱ = density of water, v = velocity of water.

Joppen and Ippen (1964) measured resistive force by empirical determinations on tethered shells. Unfortunately, since my experiments were conducted in a closed tube, it was not possible to use a similar technique. However, Stokes' law states (Collieu and Powney, 1977) that the resistive force of a spherical body (f) in a uniform velocity field is given by the equation

$$f = 6\,\pi \cdot \eta \cdot r \cdot v$$

where η = viscosity, r = radius of sphere, and v = velocity of flow.

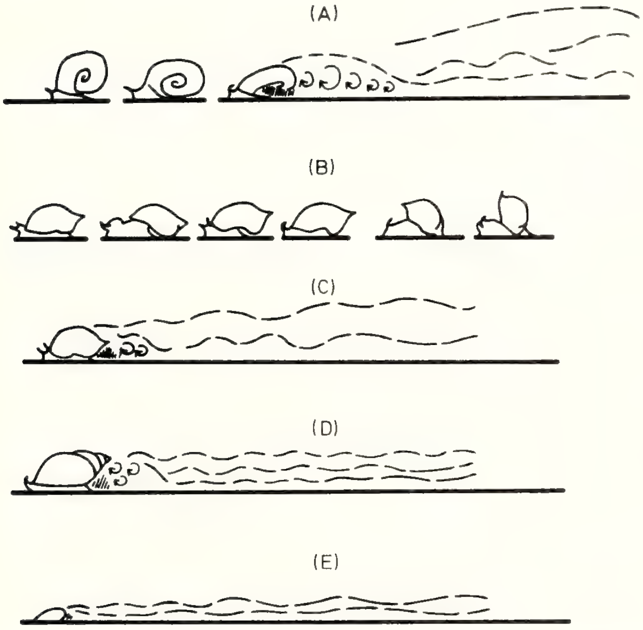

Fig. 2. Behaviour, stream lines and vortices downstream of the snails. (A) Planospiral snail changing shell position as flow increases. The last diagram shows the stream lines and vortices at maximum flow. (B) Characteristic movement of *Lymnaea peregra* as flow increases. The last diagram shows the shell position immediately before detachment. (C) Stream lines and vortices for *L. peregra*. (D) Stream lines and vortices for *L. stagnalis*. (E) Stream lines and vortices for *Bulinus jousseaumei*.

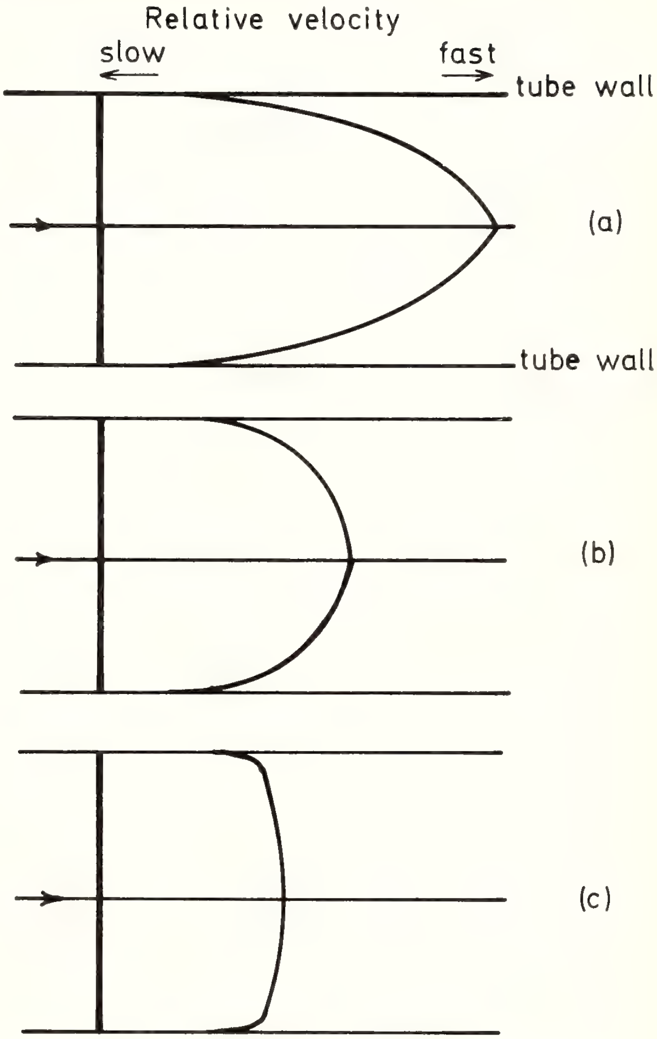

Fig. 3. Velocity profiles for (a) smooth flow, (b) transitional flow and (c) turbulent flow (after Duderstadt *et al.*, 1982).

On a snail of approximately spherical shape such as *Lymnaea peregra* and diameter of 0.006 m, $f = 6.3 \times 10^{-5}$ N. Stokes' law only applies in smooth flow and the flow here might have been just turbulent enough to negate the valid application of the law. Stokes' law also presumes that the object is free of any nearby surfaces, which is not the case here since the mollusc is attached. The drag coefficient for a typical specimen of *L. peregra* was thus calculated to be 0.0053 which compares with a value of approximately 0.6 obtained by Jobin and Ippen (1964) for *Biomphalaria glabrata*. The discrepancy is almost certainly due to the limited applicability of Stokes' law and indicates that resistive force should be measured using methods similar to those of Jobin and Ippen.

Many of the previous authors have described consistently similar patterns of behavior. For example, snails would initially move randomly, next orientate with their heads upstream and then make regular movements to pull the shell over the foot, before finally detaching. In addition to confirming these general patterns of behavior, I observed some interspecific differences. For example, the planospiral taxa (*Biomphalaria* and *Planorbis*) would initially hold the shell erect whilst facing upstream so that the shell acted like a rudder. As velocity increased, the shell would be held at an increasingly acute angle to the substratum. At higher velocities, the shell would be held parallel with and close to the substratum, in the zone of slowest water flow. The columella muscle and associated viscera would be stretched several millimetres from shell to foot mass before the snail eventually detached. Globose molluscs (*Lymnaea*) would follow the general pattern for molluscs described previously by other authors such as Jobin and Ippen (1964). In addition, after some time at high velocities, snails would first lose control of the columella muscle so that the shell would be swept downstream of the foot and would then yaw violently, with the snail periodically trying to gain control and achieving this for short periods. Eventually the part of the shell normally held over the head would lift up into the zone of fastest moving water and the snail would immediately detach. By contrast, *B. jousseaumei* clamped down, did not lose control in stages and eventually detached instantaneously. *B. jousseaumei* had a shell shape superficially similar to *L. peregra* but the shell was more glossy with a smoother profile. Data from all species tested were used to attempt to find a relationship between parameters of size and flow encountered at maximum velocity. Data were $\log_{10}$ transformed, to normalise each variable and ensure the validity of parametric statistical analysis. In almost all cases, transformation improved the significance of relationships. Multiple regression analysis of flow as $dm^3 \cdot s$ before detachment (Y) in relation to mass (X_1), foot size (X_2) and profile (X_3) of all snails gave the following equation:

$$Y = 2.42 + 0.0874X_1 + 0.242X_2 - 0.748X_3$$

(t values of 0.54 for X_1, 1.83 for X_2 and -3.35 for X_3; $F_{3,409} = 16.7$ $P < 0.001$).

Detachment flow as $dm^3 \cdot s$ was plotted against the most significant variable from the multiple regression for the data from all the species, in order to partially visualise the relationship uncovered by the mulitple regression (Fig. 4). The data showed a considerable amount of scatter, suggesting that some stochastic term needs to be included in future analyses. Nevertheless, there was a highly significant negative linear slope ($F_{1,412} = P < 0.001$) which suggested that snails with larger profiles would detach at lower flows. Further analyses therefore concentrated on the profile rather than mass or foot size.

It might be thought that the relationship between profile size and flow described above was predictable and hardly worthy of comment. However, the relationship was not always so obvious when data for individual species were selected from the data matrix and detachment flow was plotted against profile. Some taxa failed to show a relationship, probably through lack of data (e.g. *Physa fontinalis, Biomphalaria jousseaumei* and *P. vortex*). For the taxa which showed significant linear or multiple regression relationships, data were plotted in figures 5-9. A pigmented population and an albino population of *B. glabrata* were included in order to identify intraspecific variation. The planospiral snails (Figs. 5-7) showed a more obviously linear relationship than the more globose snails (Figs. 8-9).

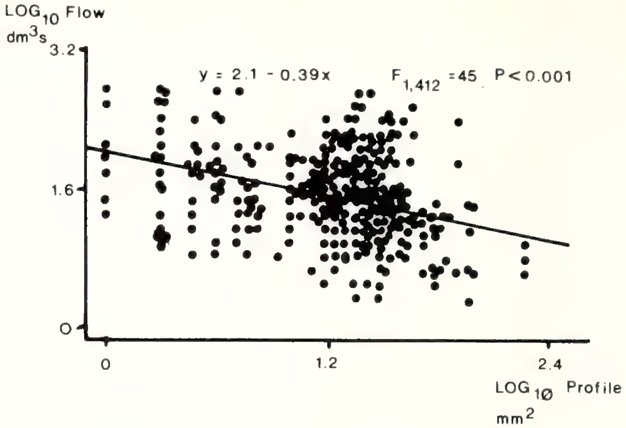

Fig. 4. Relationship between detachment flow and profile area for all snails used in these experiments.

Attempts were made to obtain a size index which would relate more closely to detachment flow than profile alone. The following relationship was used:

size = (foot size/profile) x mass.

This index gave significant regression relationships for several species, sometimes improving on the F values obtained in the regressions where profile alone had been used as the independent variable. For example, for *Planorbis planorbis* the new value was $F = 6.9$ compared with $F = 5.2$.

Of the species studied here, *Lymnaea peregra* is the most likely to encounter flowing water and so more attention was focussed on this snail. A multiple regression analysis of detachment flow on mass, foot size and profile gave a significant relationship ($F_{3,168} = 4.2$, $P < 0.01$). The regression equation is given in Table 1. No investigation of the allometric relationships between foot size, profile and mass were made, since this was not the main subject of the present study, though results of such an investigation might slightly improve the performance of the index described above by introducing a cubic power function for body mass and squared functions for foot area and profile.

Studies on *Lymnaea peregra* took place over a period of approximately 6 months, during which time snails were kept in the laboratory, and fed on boiled dried lettuce. Some snails deposited eggs during their natural egg laying period in early spring. A one-way analysis of variance was carried out on detachment flow, with time of year as the factor under investigation. A significant effect of time was found (Table 2), which could be due to the diversion of metabolic resources to egg laying during the period of study. However, data for *Biomphalaria glabrata* and *Planorbis planorbis* were available in which individual snails had been tested before and after

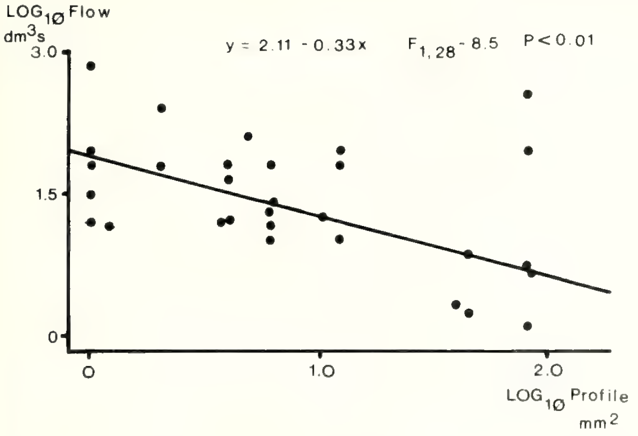

Fig. 5. Relationship between detachment flow and profile area for *Biomphalaria glabrata* (pigmented).

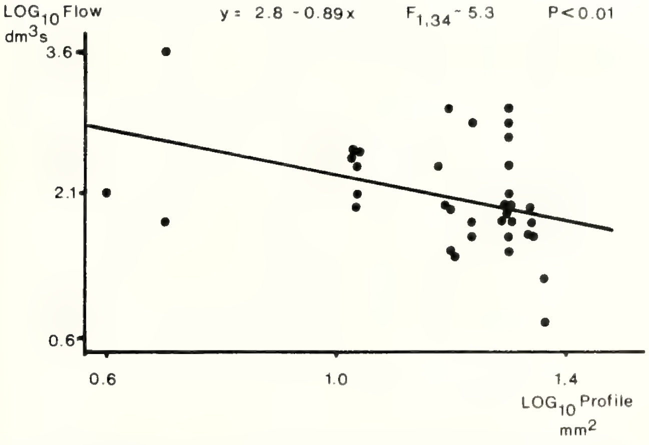

Fig. 7. Relationship between detachment flow and profile area for *Planorbis planorbis*.

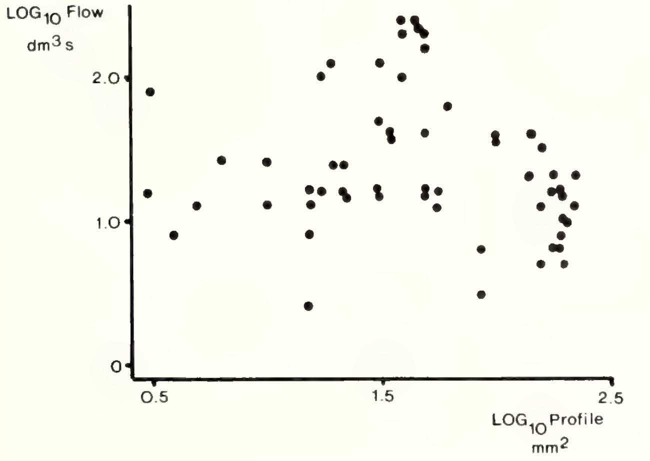

Fig. 9. Plot of detachment flow against profile for *Lymnaea stagnalis.*

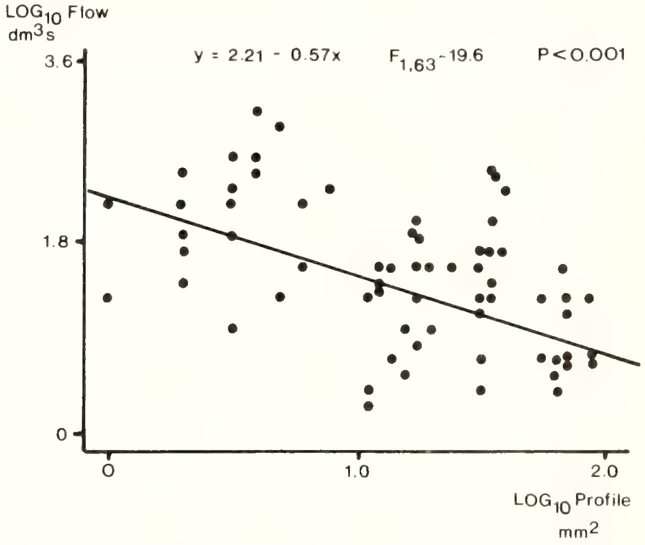

Fig. 6. Relationship between detachment flow and profile area for *Biomphalaria glabrata* (albino).

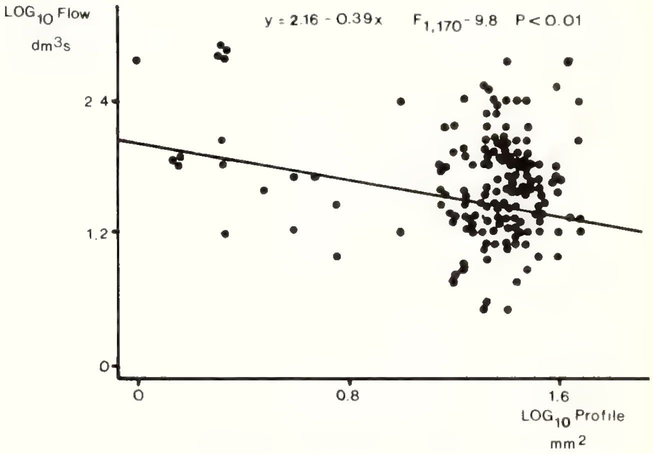

Fig. 8. Relationship between detachment flow and profile area for *Lymnaea peregra.*

egg laying. No statistically significant effects on detachment were noted but the data set was small and the experiment could be usefully repeated for these and other species.

Effects of substratum type were investigated by inserting a piece of coarse carborundum paper firmly into the test chamber. This had no measurable effect on the discharge through the pipe. No significant difference in detachment flow was noted between populations of *Lymnaea peregra* which were on the rough surface or the smooth surface of the PVC tube.

Effects of feeding were investigated by maintaining a population of *Lynmaea peregra* for one week without food prior to testing. Analysis of variance showed that food was a significant factor (Table 2). However, it was surprising to note that fed snails detached at lower velocities than unfed snails.

Table 1. Results of multiple regression analyses for detachment flow ($dm^3 \cdot s$) in relation to mass (x_1), foot size (x_2) and profile (x_3). Only snails showing significant relationships are included. All data were $\log_{10}$ transformed.

	Intercept	x_1	x_2	x_3		
All species						
Coeff.	2.42	+0.087	+0.242	−0.75	$F_{3,409} = 16.7$	$P < 0.001$
St. dev.	0.45	0.16	0.13	0.22		
Lymnaea peregra						
Coeff.	1.37	−0.296	+0.70	−0.66	$F_{3,168} = 4.2$	$P < 0.01$
St. dev.	1.14	0.41	0.43	0.54		
L. stagnalis						
Coeff.	7.66	+2.36	−0.24	−0.32	$F_{3,53} = 3.5$	$P < 0.05$
St. dev.	2.1	0.83	0.33	1.15		
Planorbis planorbis						
Coeff.	2.82	−0.036	+1.19	−1.83	$F_{3,31} = 2.9$	$P = 0.05$
St. dev.	1.52	0.58	1.11	0.68		
Biomphalaria glabrata (albino)						
Coeff.	1.18	−0.339	−0.043	−0.024	$F_{3,61} = 6.7$	$P < 0.001$
St. dev.	1.28	0.43	0.29	0.69		
B. glabrata (pigmented)						
Coeff.	−2.19	−1.90	+2.09	+0.539	$F_{3,26} = 5.7$	$P < 0.01$
St. dev.	2.13	0.80	0.86	0.84		

Effects of temperature change were investigated by keeping *Lymnaea peregra* at 4°C for several days before testing them in the apparatus at a temperature of 22°C. Analysis of variance again showed a significant effect of this factor (Table 2). Snails which had not experienced a temperature change detached at an earlier time than cold adapted snails. This experiment might have been confounded with the previous one however; although fed and unfed snails were kept at low temperature before testing, the metabolism of the snails had slowed down to such an extent that snails which did have food did not consume it. Initial analysis of the data for *L. peregra* did not find any significant relationships between detachment flow and any aspect of size. In the light of the above experiments however, data relating to the temperature and food experiments were omitted and significant relationships then appeared in the regressions.

An analysis of variance was undertaken to compare mean detachment time for all taxa investigated here. Results are given in figure 10. Although there was a highly significant variation between taxa ($F_{6,379} = 7.4$, $P < 0.001$) there was no obvious pattern in the relative means. Table 3 shows the maximum velocities endured for at least one minute by snails in my experiments by comparison with other authors. It is difficult to compare results with other authors since snail sizes are not always given. For the sake of the comparison, I assumed that mature snails had been used.

In the lifting experiments on *Lymnaea peregra* preliminary investigations showed that approximately 50 trials over 30 minutes were needed before a full sized specimen of *L. peregra* began to show fatigue. Means of 15 trials were therefore obtained but there was no relationship between size and strength. There did appear to be a possible relationship between absolute strength of *L. peregra* and it's ability to resist a flow for long periods but the relationship was not statistically significant ($F_{1,25} = 3.3$, $P < 0.10$). A similar investigation of *Planorbis planorbis* did not suggest any possible relationship. The globose *L. peregra* at an average mass of 0.273 g was able to exert an average force of 0.0385 N, approximately equivalent to 14 times it's own body mass in a vertical lift. By contrast *P. planorbis* at an average mass of 0.17 g exerted an average force of 0.019 N, approximately 11 times its' own body mass.

Table 2. Results of analyses of variance on several aspects of the biology of *Lymnaea peregra* in relation to detachment flow.

Factor	df	F	Significance
Time	1,179	4.7	$P < 0.001$
Surface	1,195	1.9	
Food	1,195	7.1	$P < 0.01$
Temperature	1,195	8.3	$P < 0.01$

DISCUSSION

Studies similar to those described here have usually employed inclined flumes, with precautions taken to minimise turbulence in the channel; the velocity of the water was changed and the number of snails detaching at each velocity was recorded. Such a design makes results difficult to interpret if snails can stay attached at the highest velocity provided. Also, snails can interact with the surface and the corners in box sectioned channels. In biological terms, the tube is much more controllable, though the physics of flow in tubes is complicated. The video camera proved to be a useful device for examining the effect of mollusc on the flow pattern in the tube. Vortices could be seen and it was noticeable that certain species such as *Lymnaea stagnalis* appeared to produce a non-expanding vortex pattern, whilst others such

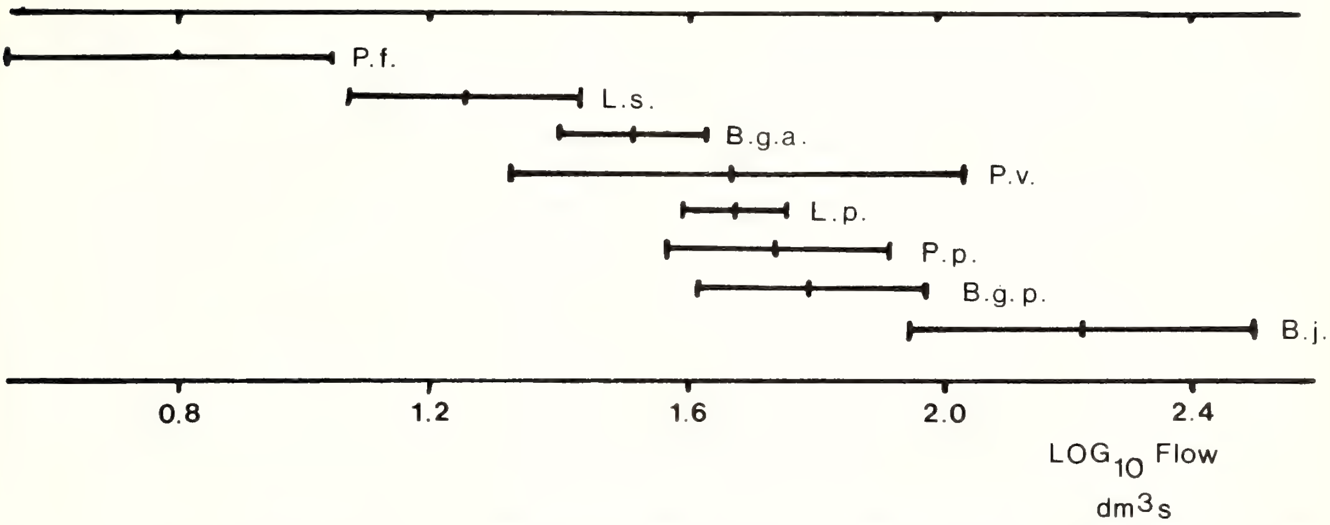

Fig. 10. Comparison of mean detachment flow for each species, together with 95% confidence intervals. An analysis of variance showed significant variation between species ($P < 0.001$). P.f. = *Physa fontinalis*; L.s. = *Lymnaea stagnalis*; B.g.a. = *Biomphalaria glabrata* (albino); P.v. = *Planorbis vortex*; L.p. = *L. peregra*; P.p. = *P. planorbis*; B.g.p. = *B. glabrata* (pigmented); B.j. = *Bulinus jousseaumei*.

Table 3. Comparison of maximum velocities endured by a variety of species investigated here and in other published work. It was presumed that results were based on performances of adult snails.

Dorier and Vaillant (1964)	*Theodoxia fluviatilis*	2.4 $m \cdot s^{-1}$
	Ancylastrum fluviatile	2.4 $m \cdot s^{-1}$
	A. capuloides	0.65 $m \cdot s^{-1}$
	Radix limosa	2.02 $m \cdot s^{-1}$
	Physa fontinalis	0.89 $m \cdot s^{-1}$
	Bithynia tentaculata	0.82 $m \cdot s^{-1}$
	Lymnaea stagnalis	0.75 $m \cdot s^{-1}$
Jobin and Ippen (1964)	*Biomphalaria glabrata*	0.65 $m \cdot s^{-1}$
Moore (1964)	*P. propinqua*	0.84 $m \cdot s^{-1}$
	Stagnicola palustris	0.80 $m \cdot s^{-1}$
Madelin (1984)	*B. glabrata*	0.33 $m \cdot s^{-1}$
Dussart (1985)	*B. glabrata*	0.86 $m \cdot s^{-1}$
	L. peregra	0.86 $m \cdot s^{-1}$
	L. stagnalis	0.70 $m \cdot s^{-1}$
	Planorbis vortex	0.86 $m \cdot s^{-1}$
	P. planorbis	0.86 $m \cdot s^{-1}$
	Bulinus jousseaumei	0.86 $m \cdot s^{-1}$
	P. fontinalis	0.66 $m \cdot s^{-1}$

as *Biomphalaria glabrata* showed an expanding vortex pattern. The use of video techniques could allow much more sophisticated analyses to be made in the future.

The drag coefficient calculated for *Lymnaea peregra* was considerably different from the value for *Biomphalaria glabrata* obtained by Jobin and Ippen (1964). Even without invoking the inapplicability of Stokes law, some differences were expected since they used an equivalent to the large profile (diameter of the snail shell) rather than the area exposed to the current. They did justify the use of this dimension since they demonstrated that their snails did not perform significantly differently from standard spheres of similar size.

Regressions of detachment flow on size showed significant relationships when there were enough data. These relationships were more obvious for planispiral snails (Figs. 5-7) than for the others (Figs. 8-9). The small profile presented to water flow was the most significant predictor for detachment time. Relationships seemed to be linear with negative slopes such that larger snails detached earlier than smaller ones. This could be because larger snails are exposed to higher velocities as their shells protrude into faster flowing water. Alternatively, larger snails may be older and therefore more frail. If the latter were true however, a relationship between size and innate strength as shown by the lifting experiments might have been expected. No such relationship seemed to exist for *Lymnaea peregra*, though there was a possible relationship between strength and the ability to resist flow. There was absolutely no relationship between these factors for *Planorbis planorbis*.

There were significant differences between curves of the flow/profile regressions for the two *Biomphalaria* species (Figs. 5-6). Of species showing significant relationships, *Planorbis planorbis* had the highest slope (-0.89, Fig. 7) and *B. glabrata* (pigmented) had the lowest (-0.33, Fig. 5). Although no significant relationship could be shown for *B. jousseaumei*, this species withstood high flows for much longer than other snails. This was obvious in the analysis of variance, which compared the mean detachment times of all taxa.

Multiple regression equations reflected the results of the linear regressions; they showed that mass and profile were usually related to detachment flow through a negative slope, whereas foot area was usually related through a positive slope.

In some cases, closer relationships were obtained by using a size index, in which the foot area/ profile relationship was modified by the mass of the snail. With a smaller profile, or a bigger foot, the snail would be able to adhere for longer. The mass variable might operate through muscle volume, enhancing attachment.

There was only a tenuous relationship between the size of *Lymnea peregra* and the flow at which it detached. It is worth noting that the planispiral species tested here are usually found in still waters, whereas *L. peregra* is found in both still and flowing waters. Most snails in flowing water would find themselves on rocks or vegetation, and therefore be able to move into local areas of low flow as necessary. Ambuhl (1962) convincingly demonstrated the existence of such zones behind boulders and Dorier and Vaillant (1954) showed that current speed could fall from 33 $m{\cdot}s^{-1}$ in the main channel to less than 10 $m{\cdot}s^{-1}$ in the centre of a *Potamogeton* stand. Nevertheless, a river snail might occasionally be exposed to high flow rates before it could find shelter, and it might therefore need some capacity to resist flow. The planispiral snails tested here may not be adapted to flowing conditions and may detach in a way which directly relates to their morphology. By contrast, *L. peregra* appeared to be better adapted to resisting detachment up to a certain limit of flow (1200 s at maximum flow rate), irrespective of size. The globose nature of the shell of *L. peregra* might confer a low drag coefficient such that physiological state, and proportion of smooth muscle in the columella muscle and foot muscle might be more important factors of detachment than size. Dorier and Vaillant (1954) classified the species they investigated into two groups; firstly 'rheobionts' including *Theodoxia fluviatilis* and *Ancylastrum capuloides* which could colonise exposed areas of moss and rock exposed to fast flows; secondly 'rheophiles' including *Radix limosa* which, although found in slower flowing conditions possessed "a strong margin of security upon which they can call in exceptional circumstances, notably spates". This observation is certainly confirmed in the present study.

More research could be done to investigate the relative importance of shape rather than size. Hughes (1979) notes that for objects in very low flows (creeping flow), streamlining may increase drag forces on the snail; at higher speeds, streamlining helps because it reduces drag by preventing the separation of flow lines downstream of the shell; conversely at high flows, surface protrusions can act as spoilers which reduce the wake and therefore reduce the drag. Such structural modifications of the shell may partly explain why the North American species *Io fluvialis* (Say) has a smooth outline in headwaters but is spinose in large rivers. Predation will of course be an important factor in governing the roughness of a shell. Interaction of predation and drag factors may explain why spinose and smooth shelled taxa can exist in the same riverine habitat. Flow characteristics of the environment can cause topological rather than structural modification of shell shape. "Fluviatile species are also influenced greatly by the circumstances of their environment, those individuals inhabiting rough or disturbed waters, rapid and turbulent streams often show a shorter spire and a more expanded and larger mouth which necessarily allows for greater clinging or adhesive power and renders the mollusk less liable to be detached and probably injured by wave violence" (Taylor, 1894).

Lymnaea peregra detachment did appear to be related to food availability and time of year. There was no pattern in the temporal relationship however, though egg laying might have been a significant factor. Contrary to the results of Moore (1964), the surface was not found to be a significant variable though the surface provided here was highly artificial.

In conclusion it appears that predictable relationships can be determined for many of the freshwater molluscan species investigated here, though the scatters are large and sufficient trials must be undertaken. Once such relationships are well understood, this experimental design could be used to investigate the hydrodynamics of shells. More practically, the influence of molluscicides on snail detachment could be investigated, as well as the possibility of pulsed flows leading to the accumulation of snails in distinct parts of the system. For example, once further basic information has been obtained, snail trapping weirs could be tested both in the laboratory and in the field, in association with molluscicide application.

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DISTRIBUTION OF FRESHWATER SNAILS: SPATIAL SCALE AND THE RELATIVE IMPORTANCE OF PHYSICOCHEMICAL AND BIOTIC FACTORS

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ABSTRACT

Traditionally, freshwater snail distributions have been explained as the result of physicochemical factors, especially calcium concentration. Yet factors operating on different spatial and temporal scales rarely have been stated explicitly and alternate explanations have not been explored thoroughly. In the following conceptual model, we suggest that different factors govern snail species composition and abundance across different spatial scales. Across biogeographic boundaries, water chemistry screens potential colonists, with some species not persisting where calcium levels are less than about 5 $mg \cdot l^{-1}$. Given adequate calcium, abundance and distribution of species among and within water bodies within a region are determined by available habitats and food, if levels of disturbance, competition, and predation are low. In temporary ponds, disturbance lowers species richness and competition. Predators such as fish and crayfish determine snail abundance and species composition among and within most permanent lakes.

In support of this perspective, we provide preliminary data from three geographic areas on two spatial scales, among and within lakes, to document the importance of disturbance, competition, food selection, and predation in structuring freshwater snail assemblages. In northern Indiana, disturbance and predation seem most important in determining snail assemblages across lake types. Within a permanent pond in southern England, snail distribution depends on disturbance and food selection. Finally, distribution and abundance of snails and predators in a large permanent lake in northern Wisconsin suggest the importance of habitat-mediated predation by sunfish, crayfish, and leeches. We are now testing the predictions of this conceptual model using laboratory selection experiments, field-cage studies, and extensive lake surveys.

Freshwater ecologists (Boycott, 1936; Macan, 1950; Russell-Hunter, 1978, Økland, 1983) traditionally have stressed the importance of calcium in determining distribution and abundance of freshwater snails. Most authors have arrived at this emphasis after studying lakes in contiguous and geologically uniform regions: the English Lake District (Boycott, 1936; Macan, 1950); the Scottish lochs (Russell-Hunter, 1978); southern Finland (Aho, 1966, 1978a, b, c;

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Aho *et al.*, 1981); and Norway (Økland, 1983). Poor in calcium-bearing rocks, these regions are dominated by soft-water lakes. Owing to a concentration of this regional approach in soft-water areas, it is not surprising that effects of calcium, i.e. absence or low abundance of snails in low calcium lakes, was noticed and stressed. Yet, among lakes with abundant snails, the variation in distribution and abundance of various species remains unexplained. We believe that ecological studies at both wider (among regions) and narrower (within water bodies) spatial scales provide a more comprehensive explanation of snail distribution and abundance. In this paper, we first review briefly the literature on the importance of water chemistry in snail ecology. We then present a statistical analysis of published data sets on snail distributions and lake characteristics in northern Wisconsin that indicates water chemistry does not adequately explain snail distributions. Finally, we generate a conceptual model, with preliminary supporting examples, that suggests the importance of abiotic factors (calcium and disturbance) and biotic factors (habitat and food selection, interspecific competition, disturbance, and especially predation) in determining among- and within-lake abundances of snails.

THE TRADITIONAL VIEW

The traditional view of snail ecology, as summarized above, implies the overriding importance of calcium, but to suggest previous authors have ignored other factors would be unfair. Russell-Hunter (1978), for example, thought that trophic state, in conjunction with calcium, primarily influenced the distribution of snails, whereas water temperature was secondary, and the role of dissolved oxygen was uncertain. Although Jokinen (1983) suggested that biotic factors be tested to determine their influence on snail diversity and abundance, dissolved minerals remain the most studied factors despite evidence that water chemistry, at best, poorly predicts species composition, abundance (Harman and Berg, 1971), and shell calcification.

Calcification is not related to calcium concentration in any simple way (Morrison, 1932; Burky *et al.*, 1979; Nduku and Harrison, 1980a; Russell-Hunter *et al.*, 1981). Though Michigan lakes with thick-shelled *Physa integra* Haldeman have thick-shelled *Helisoma anceps* (Menke) and those with thin-shelled *P. integra* have thin-shelled *H. anceps*, shell thickness and environmental calcium are not correlated (Hunter and Lull, 1977). There is a similar lack of correlation between shell calcium concentration and environmental calcium in other regions (Mackie and Flippance, 1983a,b; McMahon, 1983).

Though the exact interaction between calcium and snail abundance is unknown, calcium still provides insight into snail distributions. Aho (1966) found species in calcium-poor lakes that were previously thought to require much greater calcium (Boycott, 1936). Although Dussart (1976, 1979a,b) found species abundances related to water hardness, Økland (1983) found that gastropod diversity declined significantly only in lakes with extremely low calcium concentrations (< 5.2 mg Ca$\cdot l^{-1}$). Even given this result, at least some species thrive in very softwater lakes; Rooke and Mackie (1984) found dense *Amnicola limosa* (Say) populations in softwater (< 3 mg Ca$\cdot l^{-1}$) Canadian lakes. Systematic changes in gastropod assemblages occur across geologic interfaces of soft- and hard-water Canadian lakes and streams (McKillop and Harrison, 1972; McKillop, 1984). Using stepwise multiple regression, McKillop (1984) found concentrations of calcium, nitrate, and nitrite best predicted snail species abundances. Such findings, however, leave causality in question. The value of calcium, nitrate, and nitrite as predictors may result from positive correlations with lake productivity. These field correlational studies suggest that for some species in some regions, very low calcium can limit successful colonization once dispersal has occurred.

Both laboratory and field experiments (Williams, 1970; Thomas, 1973; Thomas *et al.*, 1974; Young, 1975; Nduku and Harrison, 1976, 1980b; Dussart and Kay, 1980) suggest a minor ecological role for calcium except at extremely low levels (< 4.5 mg$\cdot l^{-1}$) when snails are adversely affected physiologically. Clearly, at calcium levels above about 5 mg$\cdot l^{-1}$, other factors determine snail distribution and abundance.

Among other physicochemical factors, water temperature and oxygen seem most important. Temperature determines onset and termination of reproduction in most freshwater snails (Russell-Hunter, 1978) as well as developmental rates, fecundity, and voltinism patterns (Brown, 1979; McMahon and Payne, 1980; El-Emam and Madsen, 1982; McMahon, 1983). High ambient temperatures may even limit the geographical distribution of some species (Van der Schalie and Berry, 1973). Low oxygen levels may preclude some prosobranchs (Aldridge, 1983; McMahon, 1983) and the ability of pulmonates to use atmospheric oxygen provides a clear advantage in hypoxic situations (Cantrell, 1981).

In summary, most of the above mentioned studies suggest that physicochemical factors set biogeographic limits to species distributions. Biotic factors, in turn, are probably more important in determining among- and within-lake abundances (see Green, 1971; Dillon and Benfield, 1982).

SNAIL ASSEMBLAGES IN NORTHERN WISCONSIN LAKES

To evaluate the importance of abiotic variables on the distribution of snails, we analyzed previously published data sets on snail occurrences (Morrison, 1932) and physicochemical parameters (Black *et al.*, 1963; Andrews and Threinen, 1966) for 64 northern Wisconsin lakes. As many as 20 snail species from the entire pool of 35 species were found in any one lake. Lakes varied in size from 4.5-2,080 ha and had alkalinities of 1.5-81 mg$\cdot l^{-1}$.

Although number of species was positively correlated with maximum depth, shoreline length, alkalinity, and conductivity, these correlations may be explained by well known species-area relationships (MacArthur and Wilson, 1967; see also Lassen, 1975; Aho, 1978a,b,c; Browne, 1981; Brönmark, 1985b for biogeographic treatments of snail distributions), given that these factors were positively correlated to surface area. However, in a stepwise multiple regression analysis, only two of the variables, area and alkalinity, were included in the regression equation (Table 1). To investigate the importance of alkalinity when the effect of area was accounted for, we analyzed the relationship between the species-area residuals (i.e. the portion of the number of species in a lake that remains unexplained by the species-area regression) and alkalinity. A significant ($p < 0.001$), positive relationship existed between the species-area residuals and alkalinity (Fig. 1), which means that in lakes of equal size, those with a higher alkalinity had a higher number of snail species. Although this can indicate the importance of calcium in determining snail distributions, the ultimate factor could be lake productivity or some other factor correlated with alkalinity. Further, the regression only explains a small part of the variability ($R^2 = 0.19$), indicating that other factors such as biotic interactions can be important in determining snail distributions. In addition, when comparing lakes with different alkalinities we found no obvious trend in the distribution of snail genera, other than that lakes with alkalinity less than 10 mg·l^{-1} (about 3 mg Ca·l^{-1}) seemed to have a depauperate snail fauna (Fig. 2). Thus biotic factors are the most likely explanation for the

Table 1. Stepwise multiple regression analysis of physicochemical parameters (from Black *et al.*, 1963; Andrews and Threinen, 1966) and number of snail species (from Morrison, 1932) occurring in lakes in northern Wisconsin.

Variable	B	Sum of squares	F	P
Area	0.004	228.7	16.2	<0.001
Alkalinity	0.105	207.7	14.7	<0.001
Intercept	0.504 $R^2 = 0.42$			

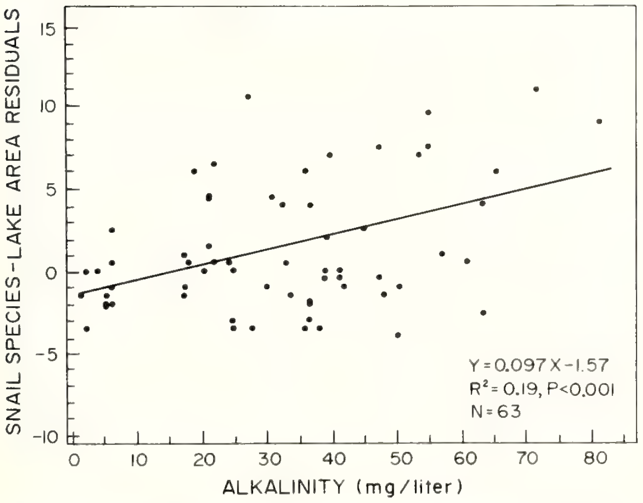

Fig. 1. Regression of snail species-lake area residuals (S*) on lake alkalinity.

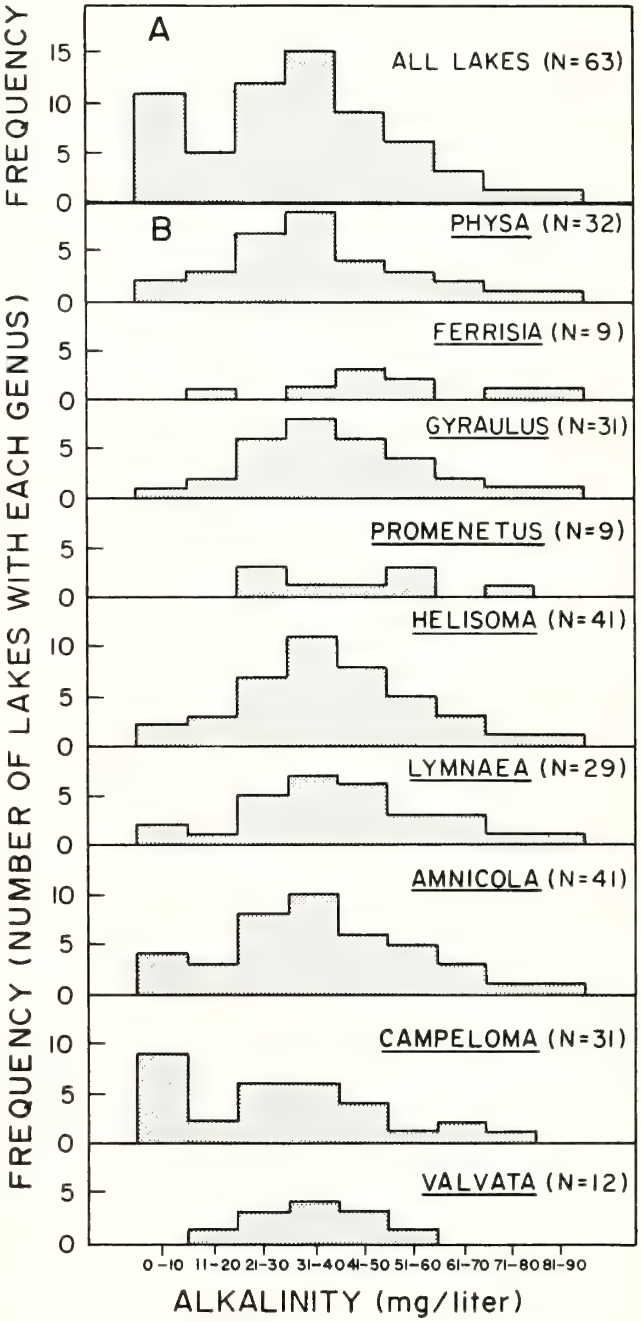

Fig. 2. **(A)** Alkalinity distribution of all lakes included in multiple regression analysis of lakes and snails in northern Wisconsin and **(B)** alkalinity distribution of lakes containing each of nine snail genera. Recent simultaneous measurements of alkalinity and calcium (Northern Lakes Long Term Ecological Research project, J. J. Magnuson, Center for Limnology, University of Wisconsin-Madison) in four of the lakes included in this analysis suggests that 10 mg alkalinity·l^{-1} (as measured by Black *et al.*, 1963) equals 3 mg Ca·l^{-1}.

distributions of snails among lakes of northern Wisconsin and in other lake regions, especially where calcium concentrations lie above 1-5 mg·l^{-1}.

A NEW CONCEPTUAL MODEL

We suggest that ecological forces act on different spatial scales and vary in importance in different water bodies. Below, we introduce those ecological factors we expect to be important across three spatial scales: (1) biogeographic scale, among geographic regions; (2) within geographic regions, among water bodies; (3) within water bodies, among habitats. We treat each of these spatial scales across the habitat continuum from temporary ponds to permanent lakes (Fig. 3). We then provide examples from our work that elucidate the relative importance of ecological factors in controlling snail assemblages among and within water bodies.

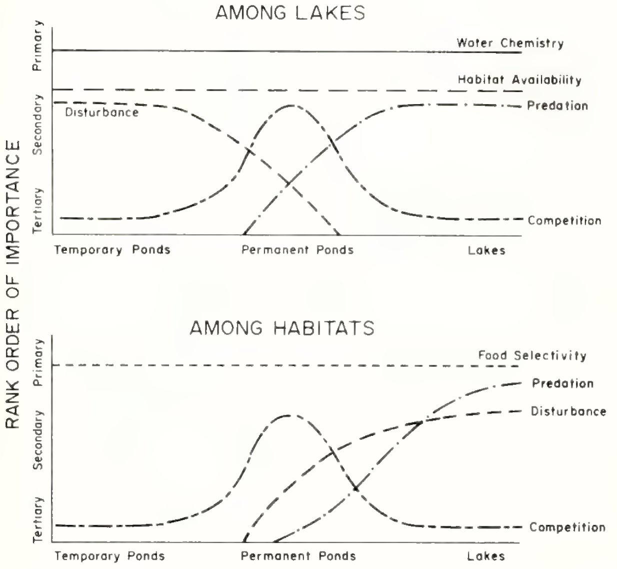

Fig. 3. Conceptual model of the importance of physicochemical and biotic factors in determining the distribution and abundance of freshwater snails on two spatial scales. The factors important in determining snail distribution and abundance in any given lake type (temporary pond, permanent pond, lake) should be understood as a heirarchy. Among habitats within a lake, for example, we expect that if food selectivity by snails does not explain the snails' distribution and abundance, then predation is the next most likely explanation. If predation is not the most important factor, then disturbance or competition probably is. A graph for "Among Regions" is not shown because we expect water chemistry is the over-ridingly important force determining differences in snail abundance on that spatial scale. Such a graph would simply have a straight horizontal line for "Water Chemistry."

COLONIZATION AND THE INFLUENCE OF WATER CHEMISTRY

The biogeographic, evolutionary history of a region determines the potential pool of snail colonizers. Several mechanisms of dispersal of freshwater snails apparently ensure colonization opportunities for all snails among water bodies within a region (e.g. Lassen, 1975). However, as reviewed above, snails cannot colonize if calcium concentration are less than 5 mg·l^{-1}. Such filtering of colonizers probably occurs across regions and to a degree within regions of very soft-water lakes.

HABITAT AND FOOD SELECTION

If calcium is adequate for snail survival, then productivity and habitat diversity of lakes may determine density and species richness within a region (Russell-Hunter, 1978). In turn, available habitat types can interact with species-specific preferences for habitat and food to determine within-lake patterns. For example, snail species diversity and substrata complexity (including macrophytes) are positively correlated in freshwater lakes of central New York (Harman, 1972). Such a relationship probably results from habitat preference (e.g. Ross and Ultsch, 1980). Macrophytes, in particular, often support a rich gastropod fauna, with snail-macrophyte associations general in some cases (Soszka, 1975; Mason, 1978; Lamarche *et al.*, 1982; Aldridge, 1983) and specific in others (Calow, 1973a; Pip and Stewart, 1976; Pip, 1978, 1985; Lodge, 1985, 1986). For ponds in southern Sweden, snail species richness and macrophyte species richness are positively correlated (Brönmark, 1985). In one case at least, specific macrophyte-snail associations result from food choice among different periphyton assemblages occurring on different macrophytes (Lodge, 1985, 1986).

Because the preferred diets of most snail species are unknown (see Calow, 1970, 1973a,b; Calow and Calow, 1975; Reavell, 1980), few predictions about specific habitat-snail associations can be made. Yet when food preference data are available, they are good predictors of species abundances in different habitats. For example, snails that prefer detritus in laboratory trials, are common in wooded ponds whereas species preferring algae are dominant in open ponds (Brown, 1982). Thus substrata and feeding preferences influence snail assemblage structure among and within lakes.

DISTURBANCE

The temporal availability of appropriate habitat and food may be critical to species persistence. Habitat disturbance (Pickett and White, 1985) can eliminate those species less able to rapidly recolonize from refuges and reproduce. Seasonal drying of temporary ponds (Brown *et al.*, 1985) and winterkill (hypoxia under ice) can be important and widely occurring sources of mortality. Snail populations also decline dramatically following reductions in macrophytes (Pimentel and White, 1959; Lodge and Kelly, 1985). Waves on exposed lake shores can also reduce snail populations much as waves on marine rocky intertidal habitats reduce the abundance of organisms (Sousa, 1984). Because such disturbances typically affect only parts of lakes or, at their broadest scale, several lakes within a region, they can contribute to the variation in snail assemblages among lakes and to differential species distributions within lakes. Rarely would local disturbances contribute to differences in snail fauna among regions.

COMPETITION

Traditionally, competition has been invoked as the major structuring force in natural communities. However, this perspective has recently been a major point of controversy, with much older evidence for competition and character displacement being called into question (e.g. Strong *et al.*, 1984). Disturbance can keep many communities in a non-equilibrium state. In such communities, population densities can never reach levels at which resources are limiting. Even in near equilibrium communities, however, predation can be the dominant structuring force (Connell, 1975). Such mechanisms clearly reduce competition in many systems (Denslow, 1985).

Laboratory experiments suggest the potential for competition among marine and freshwater snails (Fenchel and Kofoed, 1976; Madsen, 1979; El-Emam and Madsen, 1982), but field evidence is rare (Eisenberg, 1966) and anecdotal. Fenchel (1975) predicted that divergence in shell size of sympatric congeneric marine hydrobiids reduced food resource overlap. However, Levinton (1982) was unable to show differences in resource use among different sizes of hydrobiid snails. Brown (1982) investigated overlap patterns in an assemblage of four pond snails in the American midwest and found considerable divergence among species in feeding and habitat use patterns. Of the six possible pairwise interactions, overlap was high in only one. Yet even those two species inhabited temporary ponds where populations suffered dramatic mortality each year (Brown *et al.*, 1985); habitat lifespan may not have been long enough for interspecific competition to become an important structuring force.

Wiens (1984) argues that for a better understanding of important structuring factors, a spectrum of communities from non-equilibrium to equilibrium should be studied. The continuum from small temporary ponds to large permanent lakes constitutes such a set of communities. We predict that among and within water bodies, disturbance and predation reduce snail populations below densities at which competition would be important. Interspecific competition would be a major influence in permanent water bodies, and then only where other forces do not limit population size or distribution.

PREDATION

Predation is an important source of mortality for marine (Ebling *et al.*, 1964; Kitching *et al.*, 1966; Spight and Lyons, 1974; Spight, 1976; Vermeij, 1978, 1979; Palmer, 1979, 1985; Vermeij and Currey, 1980) and freshwater molluscs (Eisenberg, 1966; Gillespie, 1969; Covich, 1976, 1981; Vermeij and Covich, 1978). Marine snails have evolved thick, elaborately sculptured shells to deter their predators (Vermeij, 1978; Vermeij and Covich, 1978; Palmer, 1979, 1985; Bertness *et al.*, 1981). Although most freshwater snails have not coexisted with their predators for as long (Vermeij and Covich, 1978), large species with thick, strong shells have an advantage against predation over small, thin-shelled species (Stein *et al.*, 1984; Brown and Devries, 1985). The presence of an operculum in the prosobranchs also can serve as a defense, especially against shell-invading predators (Brönmark and Malmquist, 1986; Brown and Strouse, unpubl. data). The evolutionary significance of predation is further supported by the existence in some thin-shelled pulmonates of escape behaviors, e.g. shell shaking (Townsend and McCarthy, 1980) and leaving the water when attacked by leeches (Brönmark and Malmquist, 1986).

We expect the importance of predation to increase directly with water body size and permanence. Major predators of snails in temporary ponds are shell-invading invertebrates, e.g. sciomizid fly larvae (Eckblad, 1976), dytiscid beetles and belostomatid bugs (Eisenberg, 1966), odonates, flatworms (see Reynoldson and Piearce, 1979), and leeches (see Davies *et al.*, 1981; Young, 1981). Few data are available on the distribution patterns and predation rates of these small invertebrate predators, but most probably have low predation rates relative to those of large, shell crushing decapod crustacean and fish predators. For example, individual leeches eat fewer than one snail per night (Brönmark and Malmquist, 1986; Brown and Strouse, unpubl. data). The hemipteran *Belostoma* eats up to 10 snails per night and can dramatically reduce the populations of temporary pond snails (Kesler, pers. comm.). Individual crayfish and sunfish can eat >100 snails·day^{-1} (Covich and Klosiewski, unpubl. data). Along the continuum from temporary ponds to lakes, small invertebrate predators with low predation rates can be replaced by more effective decapod crustacean and fish predators. In a later section, we present data that suggest predation often determines among- and within-lake snail species distributions.

PARASITISM

Larvae of digenic trematode helminths are common parasites of both pulmonate and prosobranch snails (Holmes, 1983). Trematode infections can initially increase the growth rates of individual snails, but eventually depress growth and reproduction; snails with mature infections (shedding cercaria) are castrated (Wright, 1966; Hairston, 1973; Brown, 1978; Minchella and LoVerde, 1981; Minchella *et al.*, 1985). Therefore, infections can alter population dynamics, but little information is available on infection levels in natural populations of freshwater snails. Nothing is known of the effects of trematode parasites on the competitive abilities or predator avoidance abilities of freshwater snails. In populations of pulmonate pond snails in Indiana, prevalences are about 25%, and increase dramatically with the length of the snail life cycle. Under such conditions, trematodes could reduce the population growth rates of snails (Brown *et al.*, unpubl. data).

However, in Trout and other lakes in the north central lake district of Wisconsin, prevalence (percentage of sampled individuals shedding cercaria) for most snail species was $<5\%$ (Table 2). Because only these individuals are castrated, the effect on population dynamics is probably minor. However, because some species of snails (Table 2) do harbor large populations of metacercaria (resting cysts that can reinfect the same or different snail species), longer term studies of trematode dynamics in snails are necessary. Because prevalences were low for most of these lake-dwelling

Table 2. Prevalence of larval trematodes in snails in several Vilas County, Wisconsin lakes. Snails were collected in June 1984 and July 1985, isolated for 24 h at 700 footcandles, examined for emerging cercaria (C), and then crushed to recover metacercaria (M). For each snail species, trematode types are listed in order of abundance.

Species (Lake)	Year	(N)	Occurence of Trematodes (%) Cercaria	Metacerc.	Trematode Type
Lymnaea emarginata (Say)	1984	(30)	22.2	100.0	Diplostomatid (M)
(Trout)	1985	(105)	3.8	0.0	Echinostome (C), Strigeid (C), Xiphidis (C)
L. stagnalis (Linn.) (Trout)	1984	(30)	0.0	100.0	Strigeid (M), Echinostome (M), Tetracotyl (M)
	1985	(67)	0.0	10.4	Tetracotyl (M)
Helisoma anceps	1984	(30)	0.0	10.0	Echinostome (M)
(Trout)	1985	(61)	4.9	0.0	Echinostome (C), Xiphidis (C)
Physa spp.	1984	(30)	0.0	0.0	
(Trout, Mann)	1985	(73)	5.5	0.0	Schistosome (C)
Gyraulus parvus (Say) (Trout, Mann)	1985	(73)	6.8	30.2	Strigeid (C,M)
Amnicola limosa (Trout)	1985	(104)	0.0	0.0	
Campeloma decisa (Trout, Grassy)	1985	(95)	25.3	94.5	Cyathocotylidae (C), Xiphidis (C), *Leucochloridismorpha constantiae* Gower (C,M)

snails, we suggest that parasitism is not an important population regulating factor for most species in large permanent bodies of water.

THE MODEL REVISITED

In summary, we predict that water chemistry acts as a filter for colonists and probably contributes to differences in snail fauna across broad geographic boundaries. Given adequate calcium, quantity and quality of available habitat and food determines abundance and distribution of species if disturbance and predation are low. Especially in temporary ponds, disturbance keeps diversity and interspecific competition at low levels. Competition is most likely to occur in permanent water bodies where predation is low and exerted by relatively few, ineffective invertebrates. We view these conditions as somewhat special and predict that in most lake districts, more effective predators, especially crayfish and fish, are abundant and the most important source of snail mortality. The impact of predators will, however, be mediated by habitat structure. Below, we provide preliminary data on two spatial scales—among and within lakes—and from three geographic areas to document the importance of disturbance, competition, food selection, and predation in structuring freshwater snail assemblages.

AMONG LAKES: DISTURBANCE, COMPETITION, AND PREDATION

Along a gradient of temporary to permanent water bodies in northeastern Indiana, clear changes in species composition occur (Fig. 4). Pulmonates are abundant in temporary ponds and a permanent pond whereas prosobranchs are abundant in Crooked Lake, a large marl lake. These patterns are consistent with our conceptual model . Because temporary ponds are disturbance-dominated, only pulmonates that can aestivate during the annual drying cycle occur. When the pond refills, these pulmonates can repopulate, owing to their short generation times and high fecundities (see Calow, 1978; Browne and Russell-Hunter, 1978; Brown, 1983).

Prosobranchs, apparently unable to withstand dry periods, do not occur in temporary ponds. Yet alternate explanations for prosobranch absence exist: lack of colonization; competitive exclusion by pulmonates; and inappropriate physicochemical environment, especially periodic low oxygen. Although pulmonates possess characteristics that make them good "colonizers" (*sensu* Lewontin 1965), reaching a water body apparently is not a problem for any group of snails (see Jokinen, 1983). Rapid colonization of British waters by *Potamopyrgus jenkinsii* (Smith) (Bishop and DeGaris, 1976)

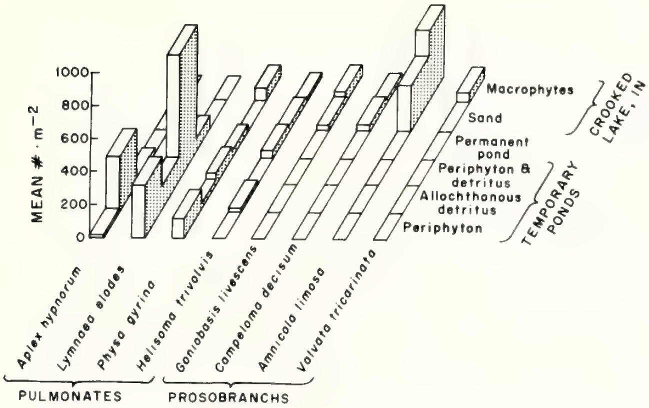

Fig. 4. Densities of snails in northeastern Indiana across water bodies differing in permanence, food resources, and predators. Temporary ponds drying earliest are at the bottom; ponds and within-lake habitats toward the top are more permanent. Fish predators occur only in the permanent pond and Crooked Lake. Snails were sampled with an Ekman grab (with minimum sample number = 10). Samples were pooled and sorted as described in Brown (1982). Ponds were sampled in June-July 1980, 1981; Crooked Lake was sampled in June-July 1983.

attests to the mobility of prosobranchs. In those prosobranchs that have life histories similar to pulmonates, populations can grow rapidly after disturbance (Lodge and Kelly, 1985). Because competition would have at most 1-3 generations during which to be effective in a temporary pond (except among those species surviving the dry period), competitive exclusion is unlikely. Finally, low oxygen could exclude prosobranchs from temporary and small eutrophic ponds. Unlike pulmonates, most of which can use atmospheric oxygen, prosobranchs are restricted to gill-breathing (see McMahon, 1983).

In temporary ponds, seasonal drying and low oxygen can exclude prosobranchs and allow pulmonates to flourish. In contrast, lake habitats, as more permanent water bodies, are generally more favorable to snails. If permanent habitats allow prosobranchs to flourish (Fig. 4), why are pulmonate densities often low? We believe that both competition and predation could be important. Unfortunately, mechanisms of competition between pulmonates and prosobranchs are not clear, and few relevant data are available.

Relative to prosobranchs, most pulmonates have a thin shell. Thus they are more susceptible to shell-crushing predators (Stein *et al.*, 1984), which are more abundant in permanent water bodies than in temporary ponds. The greater abundance of the pulmonate *Lymnaea elodes* Say in an unproductive temporary pond, relative to a productive permanent pond (Fig. 4), results from predation by the central mudminnow [*Umbra limi* (Kirtland)], which only occurs in the permanent pond (Brown and Devries, 1985). We suspect that both the general low abundance of pulmonates in permanent waters and the greater abundance of snails in general in macrophytes, relative to sand, are predator effects. In Crooked Lake (Fig. 4), pumpkinseed [*Lepomis gibbosus* (Linn.)] and redear sunfish [*L. microlophus* (Gunther)], both specialist molluscivores (see Mittelbach, 1984; Stein *et al.*, 1984), were common (Brown, unpubl. data), but macrophytes probably act as a refuge from fish predation (Crowder and Cooper, 1982; Gilinsky, 1984).

WITHIN WATER BODIES: DISTURBANCE AND FOOD SELECTION

Distributions of snails between submerged and emergent macrophytes within Radley Pond, a 0.9 ha, eutrophic pond in southern England are influenced primarily by disappearance of submerged macrophytes (Lodge and Kelly, 1985) and by selection of periphyton foods between different macrophyte types (Lodge, 1985, 1986). Of six moderately abundant gastropods in Radley Pond, five have much higher numbers per m² bottom area in one habitat, i.e., either on submerged or emergent macrophytes (Fig. 5). Even if snail densities are expressed per unit surface area of macrophytes (as per Cattaneo and Carignan, 1983), such differences in densities (1-4 orders of magnitude) demonstrate that snail distributions are not simply a product of macrophyte abundance in the two habitats.

A summerkill of submerged macrophytes (Fig. 6) reduced dramatically the densities of those snails inhabiting them (Fig. 5) whereas emergent macrophytes and associated snails changed little. With regrowth of submerged macrophytes, previous patterns of distribution and abundance recurred (Figs. 5 and 6).

Those species that inhabited the submerged macrophytes generally had shorter life cycles and higher fecundities than the inhabitants of the emergent macrophytes (Lodge and Kelly, 1985). Interaction between life history characteristics and habitat disturbance explains the absence of species with low fecundity in submerged macrophytes, but does not explain the absence of those with colonizing traits from the more permanent habitat. At least for *Lymnaea peregra* (Müller) and *Planorbis vortex* (Linn.) (diet preferences within other species were not examined), preferences for the periphyton found on their respective macrophyte substrates explain their distribution (Lodge, 1985, 1986). Neither competition nor predation are necessary to explain observed distributions.

Though shell-crushing predators are absent from Radley Pond, both invertebrate and vertebrate predators occur there. *Glossophonia complanata* (Linn.), a snail-eating leech (Wrona *et al.*, 1981), is abundant, especially in the emergent macrophytes. The mean annual density ($x \pm 1$SE, n = 20 months) of adult leeches was 117 ± 36·m^{-2} in submerged macrophytes and 182 ± 24·m^{-2} in emergent macrophytes (Lodge, 1986). Yet little is known of its predation rates or the selectivity of its feeding (Brönmark and Malmquist, 1986). The only vertebrate predator of snails in Radley Pond is the brown trout (*Salmo trutta* Linn.), but thick emergent macrophytes and the shallow water in which they grow restrict trout to submerged macrophytes. Among the snails, trout eat almost exclusively *Lymnaea peregra* (Lodge, 1986), the most abundant species in the submerged macrophytes. Radley Pond, then, demonstrates that when the

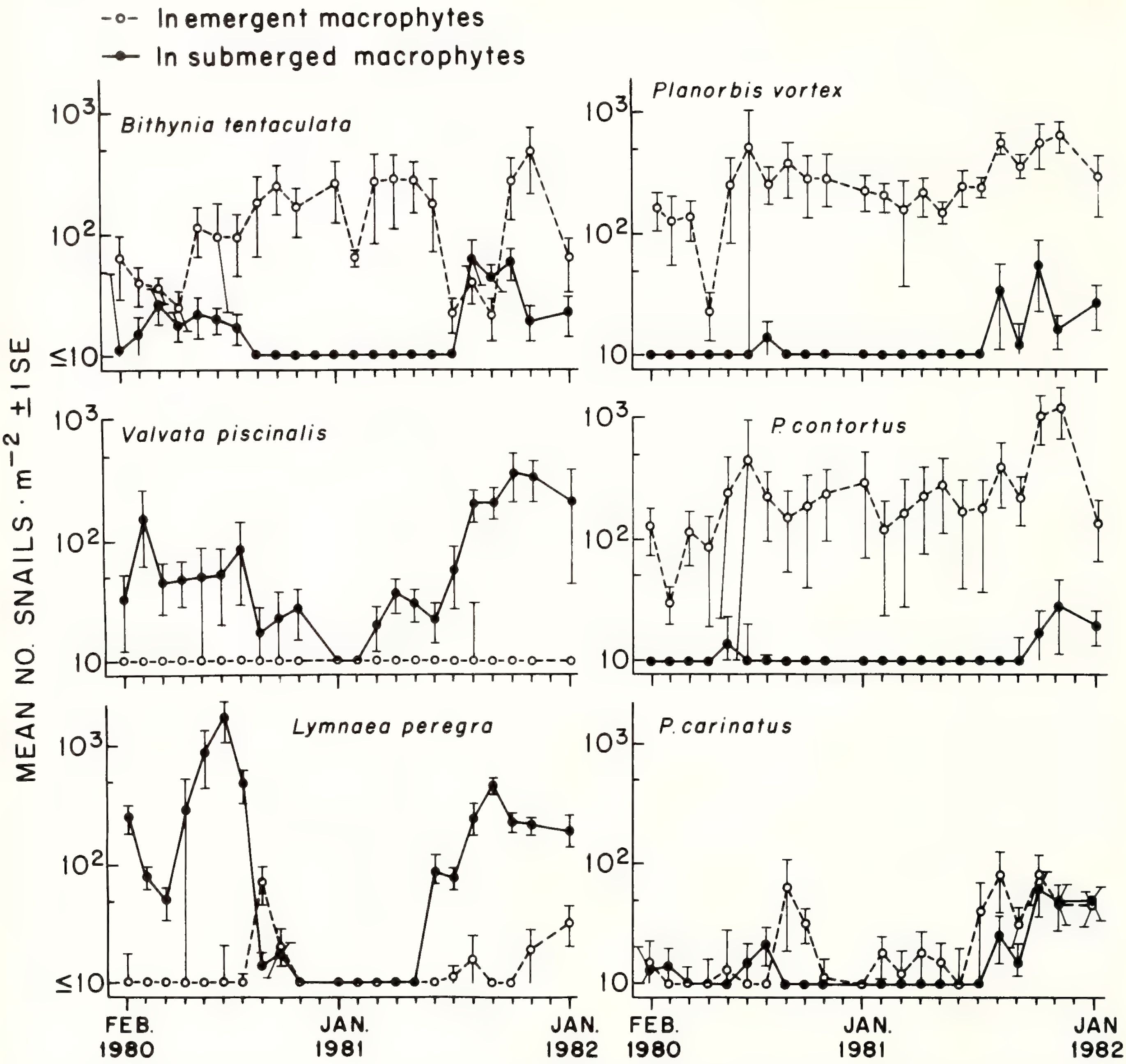

Fig. 5. Densities of snails in Radley Pond, southern England, in two neighboring macrophyte habitats, during 2 years. Submerged macrophytes were more permanent than emergent macrophytes and periphyton on the two macrophytes differed. Snails were sampled and sorted as described in Lodge (1985). Graphs for *Lymnaea peregra* and *Planorbis vortex* are taken from Lodge (1986).

magnitude of disturbance is relatively high, it has an important influence on the distribution of snails. Predation pressure is low in Radley Pond, and food preferences are expressed.

WITHIN WATER BODIES: PREDATION

We predict that in a large permanent lake with low disturbance, predation would be the major influence on snail distributions (see Fig. 3). In Trout Lake, Wisconsin, neither summerkill nor winterkill occurs, and within-lake distributions of snails and predators were negatively correlated (Fig. 7). There were three potentially important predators types: pumpkinseed (sunfish), crayfish [*Orconectes rusticus* (Girard), *O. propinquus* (Girard), and *O. virilis* (Hagen)], and leeches [*Haemopis grandis* (Verrill)]. Small snails typically exceed 60% of the diet of adult pumpkinseeds (Sadzikowski and Wallace,

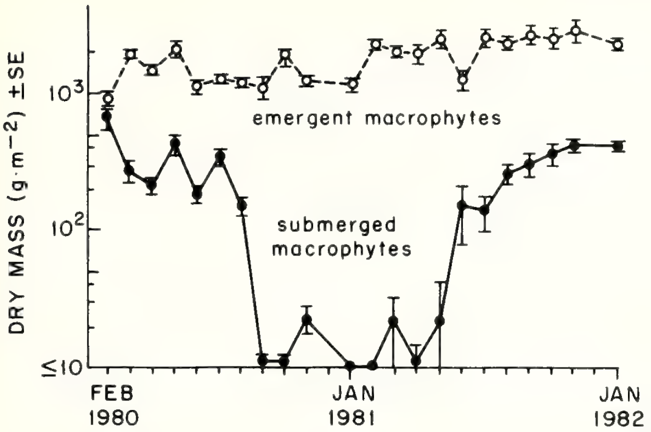

Fig. 6. Standing crop of two neighboring macrophyte habitats in Radley Pond during two years. Figure is taken from Lodge and Kelly (1985).

1976; Laughlin and Werner, 1980; Mittelbach, 1984). Crayfish are known to feed readily on snails (Covich, 1977). *H. grandis* is molluscivorous, but its distribution across habitats and feeding rates are poorly known. In Trout Lake, snail densities were highest on open sand substrates where food is apparently scarce, but crayfish and fish were virtually absent. In contrast, cobble habitats, where periphyton and crayfish were abundant, supported few snails (Fig. 7). Macrophyte habitats, where crayfish were intermediate in abundance and pumpkinseed were abundant (relative to other Trout Lake habitats), supported intermediate densities of snails. Although these preliminary data suggest that predators determine snail distribution across habitats within Trout Lake, alternate explanations, especially habitat selection by snails, and wave disturbance in cobble, certainly require testing.

SUMMARY

We have proposed a conceptual model of the factors important in determining the structure of freshwater snail assemblages. While colonization and water chemistry can be important in determining snail distribution across a large biogeographic scale, available evidence suggests disturbance and biotic factors are more important in determining distribution and abundance of snails among and within water bodies. Disturbance and its interaction with snail life histories is likely to be important among and within small water bodies. In the absence of disturbance and other constraints, habitat or food selection determines snail distributions among and within water bodies. Competition is likely to be important only in those few environments where predators are rare.

In permanent water bodies, predators can determine distribution and abundance of snails. Crayfish and fish, in particular, reach high densities in many lakes and have high feeding rates. Owing to the uneven distributions of predators across habitats within lakes, snails occur in habitats where predators do not occur, rather than in areas preferred by snails.

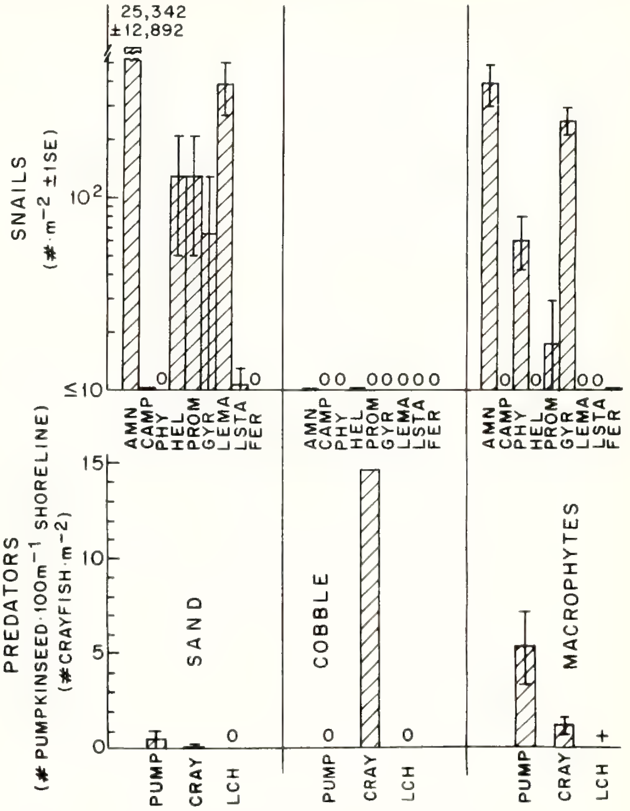

Fig. 7. Mean densities of snails and three types of snail predators (± 1 SE) in three neighboring habitats within Trout Lake, Wisconsin, June 1984. PUMP = *Lepomis gibbosus*, CRAY = *Orconectes* spp., LCH = *Haemopis grandis;* AMN = *Amnicola limosa*, CAMP = *Campeloma decisa*, PHY = *Physa* spp., HEL = *Helisoma* spp., PROM = *Promenetus exacuous*, GYR = *Gyraulus parvus*, LEMA = *Lymnaea emarginata*, LSTA = *L. stagnalis*, FER = *Ferissia* spp. Snails were sampled as follows [habitat, method (sample number)]: sand, 0.00307 m² cylindrical corer (5); cobble, 1 m² visual survey with SCUBA (5); macrophytes, 0.0127 m² cylindrical corer (18). Pumpkinseed abundance was determined by electrofishing two or three 100-m shoreline transects in each habitat. Crayfish in sand and macrophytes were counted visually in 1 m² quadrats (n = 5). Crayfish densities in cobble were taken from Capelli (1975). Relative abundance of leeches across habitats was estimated using SCUBA; plus (+) means relatively abundant, zero (0) relative rare. Biomass of macrophytes (predominantly *Potamogeton* spp., *Megalodonta beckii* (Torr.), *Vallisneria americana* Michx.) in macrophyte habitat was about 100 g dry mass·m⁻²; in sand habitat, biomass was about 10 g dry mass·m⁻² (predominantly *Isoetes* sp.).

Our conceptual model is largely consistent with available data. Most of these data are preliminary, and primarily meant to provide a basis for further work. Specifically, we require information on 1) feeding preferences and habitat choice by snails in the absence of predators, 2) snail choice and consumption rate of predators, and 3) the impact of parasitism. With these data in hand, sampling snails and predators across habitats within many lakes in a lake district will permit us to assess the validity of our conceptual model of snail distributional patterns.

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HYDROCHEMICAL FACTORS LIMITING THE DISTRIBUTION OF *BULINUS TRUNCATUS* (PULMONATA: PLANORBIDAE)

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ABSTRACT

While extremely low calcium to magnesium ratios sometimes exclude the presence of *Biomphalaria* spp., at 53 sampling stations in the south Tunisian schistosomiasis distribution area, these ratios are in a range that evidently does not exceed values tolerated by *Bulinus truncatus* (Audouin). Only very high concentrations [$Ca^{++} > 425$ ppm; $Mg^{++} > 135$ ppm; $Cl^{-} > 600$ ppm; electrical conductivity (18°C) > 2440 μmho] were avoided. The Ca/Mg ratios in Tunisia were between 0.63 and 3.4. Laboratory snails showed a significant decrease in egg laying rates in Ca/Mg from 0.5/1 to 0.2/1, and to nil at 0.1/1. Ratios were varied by addition of $MgCl_2$ to a synthetic medium containing 100 ppm calcium and the other main ions at world mean ratios. Long term maintenance (over 1/2 year) of snails at ratios $< 0.75/1$ resulted in a cessation of reproduction. When the Ca/Mg ratio (meq/meq) was kept constant at 3.65, which is the world mean ratio, and the absolute chloride concentration was raised by addition of appropriate amounts of the chlorides of calcium and magnesium, the egg laying rates remained high, up to 334 ppm, but significantly decreased in chloride concentrations of 866 and 1752. Natural water from Gabès, where *B. truncatus* did not occur, prevented egg laying and was lethal to experimental snails. It became suitable for egg laying by dilution with deionized water. It is concluded that high absolute concentrations of electrolytes, particularly chlorides, limit the distribution of *B. truncatus* in Tunisia and probably in other arid countries. A chloride concentration of about 600 ppm appears to form the upper threshold, as judged from both field and laboratory findings. *B. truncatus* appears to tolerate dissolved calcium and magnesium at relatively high levels, while *Biomphalaria pfeifferi* (Krauss), and probably other *Biomphalaria* species, prefer soft to medium hard water. In Tunisia, several freshwater prosobranch snails are able to live at yet higher electrolyte contents (electrical conductivity up to 10500 μmho; Ca^{++} up to 626 ppm; Mg^{++} up to 220 ppm; Cl^{-} up to 3900 ppm). Prosobranchs have probably maintained physiological capacities similar to their marine relatives, whereas freshwater pulmonates have attained a greater physiological distance from their marine ancestors.

The calcium to magnesium ratio in water is, as a rule, much greater than 1/1 in temperate climates. When it is extremely low, e.g. in dolomite areas, it can exclude the presence of schistosome host snails. Harrison *et al.* (1966) found this to be the case for *Biomphalaria pfeifferi* (Krause) in Zimbabwe. The adverse effect was not caused by high absolute magnesium concentration. Addition of calcium chloride brought the ratio to balance (weight ratio, corresponding to an equivalent rate of 0.6/1 and rendered the water suitable for the snails as expressed by significant increases in egg laying rates.

The existence of magnesite mining in Tunisia led us to examine the variation of Ca/Mg and its potential influence on the presence or absence of *Bulinus truncatus* (Audouin), a schistosome snail host. Other possible factors limiting distribution were also examined.

MATERIALS AND METHODS

Bulinus truncatus were reared from stocks collected by D. Haas in Gafsa (34°28′N, 8°43′E), central Tunisia, March 1970, and by J. Rutschke in Arak Bordj (25°20′N, 3°46′E), Algerian Sahara, February 1979. Laboratory studies were performed in 1970/71 on Tunisian snails and in 1981/82 on the Algerian stock.

Culture media for the examination of varied Ca/Mg ratios were obtained by adding appropriate quantities of magnesium salts to synthetic standard freshwater (SFW 100, containing 100 ppm calcium; for other details of composition of this medium, which represents world mean ratios of main ions, see Meier-Brook, 1978). Since magnesium carbonate is unstable and unobtainable, variation of magnesium concentration was achieved with $MgCl_2$ or $MgSO_4$. Snails were

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reared and used in the studies in SFW 100 at 25 ± 1°C and with a 12/12 hr light-dark regime. Fresh lettuce was fed daily *ad libitum*. Media were changed once a week unless otherwise stated. Media were aerated through hypodermic needles connected to an aquarium pump.

Snails were collected and water sampled in spring 1970 and 1971. Hydrobiid taxonomy follows that compiled by Boeters (1976). The 64 sampling stations were located in five areas in southern Tunisia, mainly around Chott Djerid, which itself seems to be free of mollusks (see Haas, 1973). Temperature, pH (Metrohm E 444), alkalinity and total hardness (Titriplex A Merck) were determined immediately; electrical conductivity at 18°C (wtw. L.F. 54), calcium, magnesium (both Titriplex), and chloride ($AgNO_3$ titration, indicator K_2CrO_4) in the laboratory in Tübingen. Carbonate hardness was calculated from alkalinity values.

RESULTS

Although the egg laying rate (Fig. 1) in the Sahara strain (Algeria) was very low, there is a tendency to reduce egg laying in Ca/Mg ratios below 0.75 down to zero at 0.1. When the Ca/Mg ratios were varied by adding the sulphate of magnesium, egg laying was further reduced to values as low as 0.0007 in 0.1/1 to 0.08 in 3.65/1. The Tunisian strain, on the other hand, had a considerably higher egg laying rate (Fig. 2). A non-significant increase occurred when $MgCl_2$ was added up to a ratio 1/1. A ratio of 0.5/1 resulted in egg laying rates almost equal to that in standard freshwater (SFW, ratio 3.65/1). A significant (t-test: $p<0.05$) decrease in rate occurred at the ratio of 0.2/1, and in 0.1/1 (the replicate only) no eggs were laid.

Long-term maintenance over 17 weeks, with a final reading after 27 weeks (Fig. 3) eventually yielded, despite heavy fluctuations, a decrease of survivorship with Ca/Mg ratios (varied by $MgSO_4$) below 1/1 and an extinction, after the ninth week, at 0.1/1. At the end of the experiments reproduction had ceased at ratios of 0.5/1 and less.

From sampling stations in Tunisia where the water had

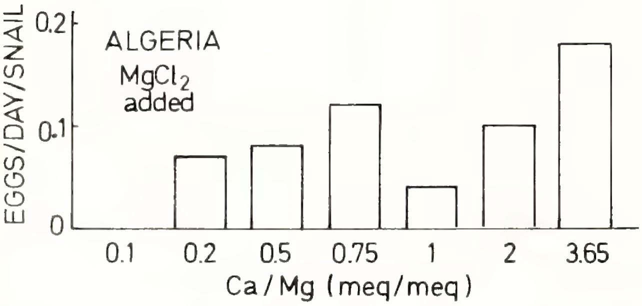

Fig. 1. Egg laying rates in Algerian *Bulinus truncatus* in artificial media with varied Ca/Mg ratios. Four beakers with 125 ml medium and 6 snails of 6 to 7 mm height each. Ratios varied by addition of $MgCl_2 \cdot 6 H_2O$ to SFW 100. Total chlorides are (from 0.1 to 3.65): 1752; 866; 344; 216; 157; 68; 28 ppm. Mean values of counts over four weeks.

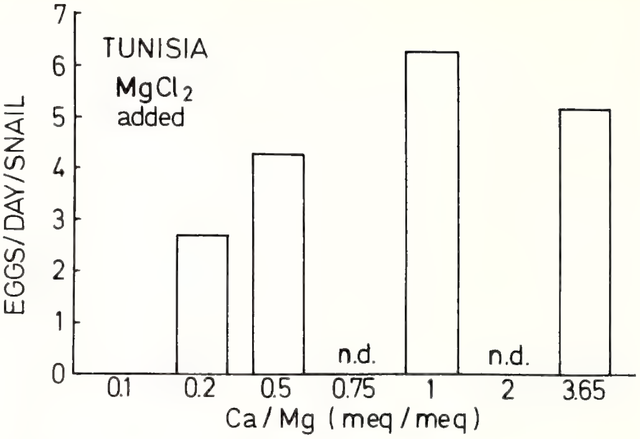

Fig. 2. Egg laying rates in Tunisian *Bulinus truncatus* in artificial media. One replicate. Ratios varied by addition of $MgCl_2 \cdot 6 H_2O$ to SFW 100 (0.1/1 only in the replicate). Total chlorides see figure 1. Mean values of counts over three or (replicate) four weeks, 4 x 4 snails, 8 to 9 mm high, in 100 ml medium each.

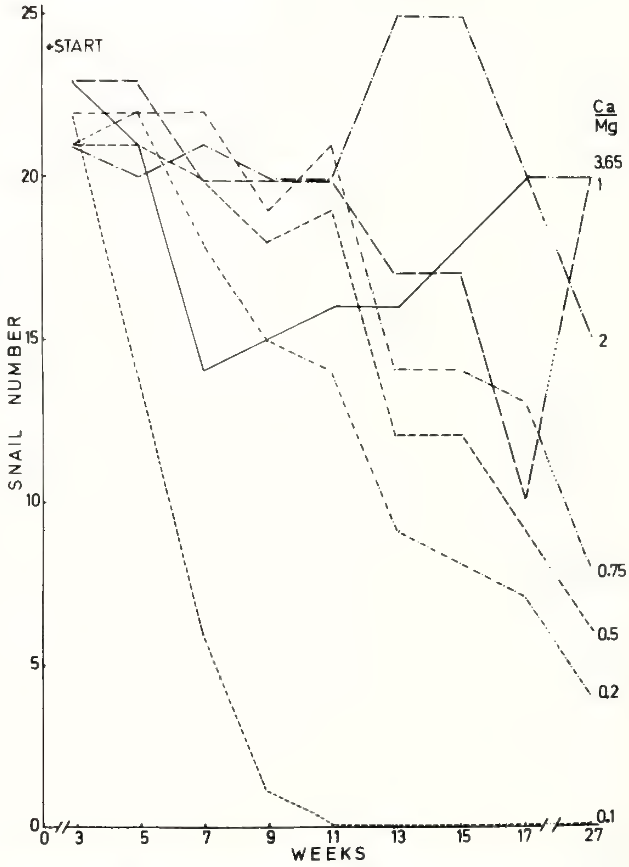

Fig. 3. Population development in Algerian *Bulinus truncatus* in artificial media with graded Ca/Mg ratios. Ratios varied by addition of $MgSO_4 \cdot 7 H_2O$. Every two weeks all snails of > 2 mm maximum diameter were counted. Sums of counts in 4 beakers containing 125 ml of medium and snails of 2 to 3 mm initial diameter. Total sulphates are (from 0.1 to 3.65): 2396; 1195; 475; 315; 235; 115; 60.5 ppm.

Table 1. Occurrence of Tunisian gastropods according to total electrolytes expressed as electrical conductivity (μmho at 18°C).

Species	Range	1220 - 2500	- 5000	- 10500
Bulinus truncatus	1220- 2440	25/42	0/7	0/4
Mercuria confusa (Frauenfeld) and *M. punica* (Letourneux and Bourguignat)	1220-10500	27/42	6/7	3/4
Hydrobia aponensis Martens	1220-10500	27/42	4/7	3/4
Melanoides tuberculata (Müller)	1220-10500	32/42	6/7	3/4
Melanopsis spp.	1550- 3580	19/42	4/7	0/4

Table 2. Occurrence of Tunisian gastropods according to total chloride concentration (ppm).

Species	Range	120 - 700	- 1500	- 3900
Bulinus truncatus	120- 602	25/45	0/6	0/2
Mercuria confusa and *M. punica*	120-3900	29/45	5/6	2/2
Hydrobia aponensis	120-3900	28/45	4/6	2/2
Melanoides tuberculata	120-3900	33/45	6/6	1/2
Melanopsis spp.	132- 956	19/45	3/6	0/2

a distinctly bitter or salty taste and *Bulinus* was not encountered, no analyses were done. Of the 53 stations where chemical data are known, only two were free of any mollusks. Within the ranges of analysis values, *Bulinus* was limited only in (1) high total electrolyte contents (expressed by electrical conductivity, Table 1) with an upper limit of 2440 μmho, and (2) high chloride concentrations (Table 2), the highest tolerated value being 602 ppm. As to these chemical characters all the commonly occurring prosobranch snails much exceeded the *Bulinus* threshold.

The calcium to magnesium ratios (Fig. 4) lying between 0.63/1 and 3.4/1 at the 53 stations obviously did not reach beyond the range tolerated by *Bulinus* in nature. Only the extremely high absolute concentrations of these cations (Ca >21 meq/*l* $=$ 425 ppm; Mg >11 meq/*l* $=$ 134.5 ppm) were avoided by *Bulinus*. The upper limit of carbonate hardness (total range 1.4 to 8.6 meq/*l*) where *Bulinus* lived was 4.7 meq/*l*.

Water from a sampling station near Gabès, Tunisia, where *Bulinus* did not occur, was brought to the laboratory and checked for its effect on Tunisian *Bulinus* snails. The water had an electrical conductivity (18°C) of 5200 μmho; calcium 23.5 meq/*l* = 471 ppm; magnesium 18 meq/*l* = 220.5 ppm; iron 0.03 ppm; carbonate content 4.8 meq/*l*; chloride 1118 ppm; nitrate - nitrogen 1.1 ppm; (the sulphate determination yielding 432 ppm was unreliable and should be neglected).

Snails were acclimatized to this water by passing them through three grades of dilution (original water/deionized water 50%, 75%, 85%) for 2 or 3 weeks each. In 100% water *Bulinus* snails survived for no more than one to two days (one snail eight days) and did not lay eggs. Simple dilution of original water with deionized water (Fig. 5) permitted egg laying, and the egg laying rate increased up to the ten-fold dilution where the medium contained one tenth of the values mentioned above.

In a last series of experiments the egg laying rate was examined in an artificial medium, where the Ca/Mg ratio was kept constant at 3.65/1 and the total electrolytes were raised by adding the chlorides of calcium and magnesium (Table 3). Egg laying rates were high in SFW 100 and remained at that level until the total electrolyte content was raised to more than 16.5 meq/*l* and a chloride concentration of 334 ppm. During the experiment (54 days) one snail died in group 3, and 4 snails died in group 4.

DISCUSSION

The very low egg laying rates in the Algerian snails may be considered strain-specific. This is mirrored by the low numbers of eggs per mass, which was about 2 to 3. For comparison, in the Tunisian strain the number of eggs/egg mass is about 11. In Fayoum, Egypt, it is about 8. These differences can be partially due to differences in snail size. Low reproductive rate in the Algerian strain, nevertheless, obviously does not hamper maintenance, as indicated by the successful rearing of these snails in tap water for 6 1/2 years,

Table 3. Egg laying rate of *Bulinus truncatus* in SFW 100 with addition of chloride but constant Ca/Mg ratio (3.65/1). 4 x 4 snails, 7 mm high, in each group. Egg numbers from 54 days of observation. Tunisian strain.

Group	Total Electrolytes Meq/l	Approximate Electrical Conductivity	Achieved by Adding Meq/l		Total Chloride ppm	Eggs/Snail/Day	Eggs/Egg Mass x ± s.d.
			$CaCl_2$	$MgCl_2$			
0 (Contr)	7.88	470	—	—	28	2.42	4.67 ± 0.55
1	11.51	900	2.85	0.78	157	2.38	5.05 ± 0.53
2	16.51	1500	6.77	1.86	334	2.54	5.10 ± 0.39
3	31.51	3300	18.55	5.08	866	1.12	2.96 ± 0.61
4	56.51	6300	38.17	10.46	1752	0.34	3.54 ± 0.37

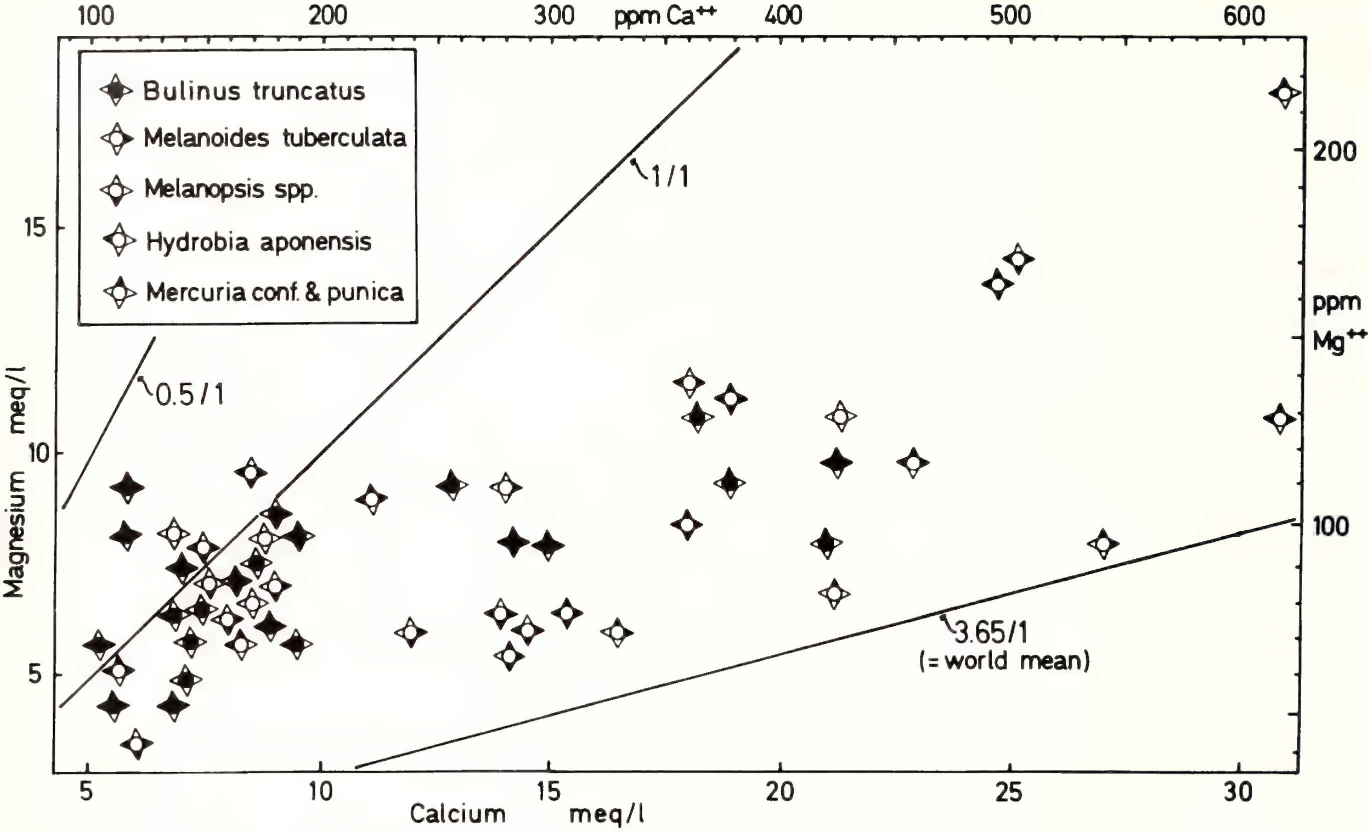

Fig. 4. Absolute calcium and magnesium concentrations and ratios in relation to gastropods collected at 53 sampling stations in southern Tunisia (1970 and 1971, both in spring).

where only three or four eggs per mass is normal.

Increased sulphate content more adversely affects egg laying than increased chloride content. Due to the lack of sulphate determinations in the field study, however, one cannot decide whether or not this anion limits distribution of *Bulinus truncatus* in Tunisia.

Adjusting the Ca/Mg ratios by adding magnesium as a chloride, though evidently better tolerated, primarily does not permit a decision as to whether the decrease in egg laying rates below the Ca/Mg ratio of 0.75/1 (Algeria) or 0.5/1 (Tunisia) was caused by an adverse Ca/Mg ratio or by the increased chloride concentration.

In regard to the Ca/Mg ratios, field distributions (Fig. 4) clearly demonstrate that all Tunisian water samples lie in a range between 3.4 and 0.63. This does not reach the experimentally determined value found to form the threshold for "normal" *Bulinus* reproduction (Fig. 2).

An effect of increased chloride concentration, using the same chloride amounts as in the Ca/Mg ratio variation, but a constant Ca/Mg ratio of 3.65/1, on the other hand, clearly shows that the significant drop of egg laying as well as eggs/mass lies between 334 and 866 ppm chloride. The highest field value in *Bulinus* habitats, 602 ppm, is in the same range. The upper limit in West Lybia, as found by Vermeil *et al.* (1952) (quoted by Deschiens, 1954), is in the same order

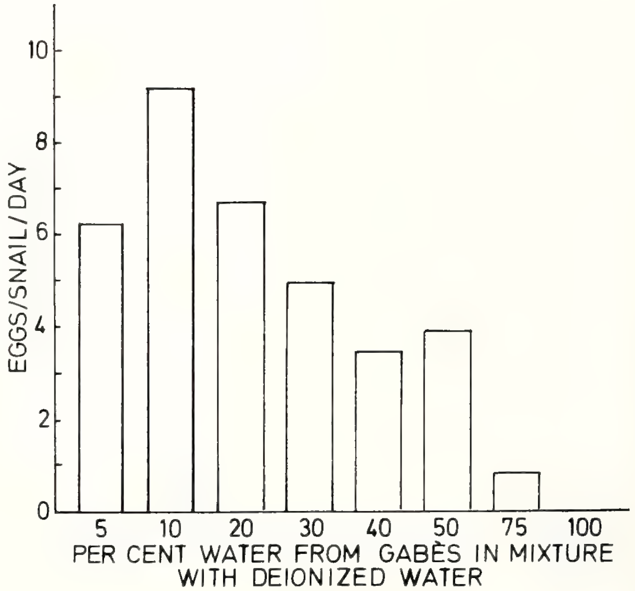

Fig. 5. Egg laying rates of *Bulinus truncatus* in original water from a *Bulinus* free irrigation canal north of the oasis of Gabès and in a series of dilutions. Mean values of counts over three weeks. Other conditions as in figure 2. Differences are significant (t-test: $p < 0.05$) between 75 and 50% and between 50 and 10%.

of magnitude, viz. between 530 and 980 ppm chloride, although Deschiens also quoted Marill (1953) who claimed to have encountered *Bulinus* in Algeria at a chloride content as high as 1530 ppm.

Chloride concentration of SFW was increased by adding $CaCl_2$ and $MgCl_2$ instead of NaCl, as usually done (Chu *et al.*, 1968; El Hassan, 1974, who used monoionic media that were completely nonphysiological), because high differences between total and carbonate hardness ("permanent" hardness) in Tunisia suggest that considerable amounts of calcium and magnesium occur in the form of chlorides and sulphates. Sodium, which was not determined due to the then inadequate analytical facilities, can therefore be present only in minor amounts. Similarly, the significant increase of the egg laying rate in the dilution series with water from Gabès (Fig. 5: 75% to 50%) was encountered when the chloride concentration dropped from 838 to 559 ppm. The natural upper limit of 602 ppm chloride lies between these two values. What ever significance may be attributed to the chloride for *Bulinus*, it must not be seen as isolated. The high absolute contents of total ions certainly play a role in limiting the distribution of *Bulinus* in Tunisia, and probably in other arid countries as well. This is indicated by the further increase in the egg laying rate after further dilution (Fig. 5), even far below the chloride threshold of around 600 ppm.

When electrolyte concentrations in Tunisia are compared with those in habitats of schistosome host snails of Africa south of the Sahara, the high levels in the arid zones are in a range that is certainly not tolerated by other species. In the Rhodesian "stream 1" of Harrison *et al.* (1966), where *Biomphalaria pfeifferi* was absent, not only was the calcium to magnesium ratio extremely low, viz. 0.05/1 (i.e. 5:62 ppm), but the water was also at the border between soft and medium, (*sensu* Williams, 1970). It contained no more than 5 ppm calcium whereas the "softest" water in Tunisia contained 97 ppm. Modifying standard freshwater (with 100 ppm Ca^{++}) to a ratio of 0.05/1 would have been possible. However, it would have meant a rise in the absolute electrolyte content to an unrealistic level. With the egg laying rates of *Biomphalaria pfeifferi* in their "stream 2" water, Harrison *et al.* (1966) demonstrated the role of absolute hardness. This water had a Ca/Mg ratio of 0.03/1 (i.e. 5.3:104.5 ppm). But while addition of $CaCl_2$ to stream 1 water up to 62 ppm (resulting in an equivalent ratio of 3.1/5.1 = 0.61) led to an increase from about 6 to 23 eggs per snail per fortnight, they did not succeed in raising egg laying in stream 2 water by adjusting the calcium content up to 104.5 ppm (corresponding to 5.2/8.6 = 0.61 equivalent ratio). In the original water the egg laying rate was nil, in the "adjusted" medium no more than 1.8 per fortnight. From this and other results (maximum respiration at 14 ppm calcium, Harrison, 1968; highest r_m-values at 12 ppm, Harrison *et al.*, 1970) they concluded that "medium" water (Williams, 1970; 5-40 ppm Ca^{++}) is optimal for *Biomphalaria pfeifferi*. A preference for soft to medium water may explain why *B. pfeifferi* do not live in arid climate zones as does, e.g. *Bulinus truncatus*.

Whether other species of *Bulinus* are adapted to hard or extremely hard water, as indicated by *B. truncatus*, must be examined. It is conspicuous, however, that some of the East African lakes, where transmission of only *Schistosoma mansoni* Sambon occurs, have low calcium concentrations, besides very low Ca/Mg ratios: Lake Albert (about 10 ppm Ca^{++}, Ca/Mg ratio about 0.18, Talling and Talling, 1965), Lake Edward (about 15 ppm Ca^{++}, Ca/Mg ratio about 0.16), Lake Victoria (about 10 ppm Ca^{++}, Ca/Mg ratio between 1.3 and 1.9). In the two former lakes *Bulinus* s.l. seem to be absent or at least rare (Dawood and Gismann, 1956), although these lake areas are not left vacant from shading in maps given by Brown (1980) for the *africanus* and the *truncatus* groups. Although generalizing ecological data (as suggested by the presence of several species of *Biomphalaria* in the Great Lakes, e.g. *B. stanleyi* (Smith), *B. smithii* (Preston), plus *B. sudanica* (Martens), and *B. choanomphala* (Martens), can lead to oversimplification, one may dare to say that *Biomphalaria* prefers rather soft to medium hard water, probably far below 100 ppm calcium, whereas *Bulinus* not only prefers hard water but also tolerates very hard waters, up to 425 ppm Ca^{++} (Fig. 4). Beyond these limits *Biomphalaria* and *Bulinus* spp. are probably no longer able to cope with osmoregulatory difficulties. The prosobranch snails (Fig. 4), which are regularly encountered in nearly all types of water bodies in southern Tunisia, evidently have no problems with the high chloride and total electrolyte concentrations (see Tables 1 and 2, Fig. 4). It can be speculated that the prosobranch freshwater snails do not show the physiological distance from their marine relatives that have been attained by freshwater pulmonates.

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COMPARATIVE LIFE HISTORY TACTICS AND SEXUAL STRATEGIES OF THE FRESH AND BRACKISH WATER BIVALVE FAUNA OF HONG KONG AND SOUTHERN CHINA

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ABSTRACT

Relatively few bivalve species inhabit the various components of the fresh and brackish water environment of southern China, including Hong Kong. Of these, the Corbiculacea are the most diverse, accounting for 7 of the 11 known species. Three unionids occur in southern China but only one, *Anodonta woodiana*, is found in Hong Kong. The Mytilidae are uniquely represented by the freshwater *Limnoperna fortunei.*

Hong Kong habitats are relatively diverse resulting from proximity to the Pearl River estuary and to the establishment of man-made habitats, i.e. reservoirs and slow flowing agricultural ditches and furrows. Two species groups, both definable as K-selected, respectively colonise large permanent lotic or lentic habitats or small lentic environments with predictable perturbations. Representatives of the former are typically dioecious (there also being a greater proportion of females and a small percentage of hermaphrodites), long lived (> 10 years), with one reproductive season each year which can be correlated with major seasonal climatic and hydrological events. They are all iteroparous and nonbrooding, except for *Anodonta woodiana.* An opposite situation is seen in occupants of small lentic, relatively stable, habitats, in which the effects of seasonal drying are more pronounced and yet still "predictable". These species are typically small, short lived (< one year), simultaneous hermaphrodites, generally semelparous and with brooding and reproductive timing correlated less with major climatic events, than with locally important environmental perturbations, probably permitting great interpopulation variability.

A third category of bivalves, typified locally by *Corbicula fluminea*, and to a lesser extent *Limnoperna fortunei,* lives for two to three years and can be broadly defined as r-selected species. These occupy a wide range of lotic and lentic, and perennial and ephemeral habitats often with unpredictable major perturbations. In the case of *C. fluminea* a variety of sexual expressions are assumed in different habitats and fertilised eggs are ctenidially brooded. This species is polymorphic with regard to shell form and colour and, most important, sexual expression. I believe that high genotypic variability and phenotypic plasticity may characterise this hitherto little-studied category of highly opportunistic and recent bivalve colonists of the freshwater domain, accounting not only for their success but also the plethora of species names attributed them.

For a number of years, I have been researching the fresh and brackish-water bivalve fauna of Hong Kong and southern China. Lack of detailed information regarding the habitat distribution of many mainland species, notably members of the Unionacea, precludes detailed discussion of them, other than to record some of them as southern Chinese species. For those species found in Hong Kong, however, including two species of Pisidiidae not hitherto investigated from continental China, enough basic information on life history tactics and sexual strategies is available to allow some important generalizations to be made.

This study therefore summarises available information on a guild of fresh and brackish water bivalves, some occupying similar, others different, habitats in Hong Kong. It attempts to demonstrate that the bivalve fauna of this subtropical place is divisible into three categories, broadly identified by application of the deterministic K- and r- selection theory to life history tactics (MacArthur and Wilson, 1967; Pianka, 1970).

Each group of bivalves possesses broadly similar reproductive strategies and is encompassed by a suite of life history traits appropriate to the broad characteristics and

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temporal stability of the environment inhabited. Although agreement is with Burky (1983) that current theoretical generalizations may be inappropriate or inadequate when applied to most populations of freshwater bivalves (especially where, as in China, such comparative information is virtually nonexistent), it is hoped that this study will provide a conceptual framework for comparison with studies of better-known faunal assemblages made elsewhere.

CLIMATE, GEOMORPHOLOGY AND HYDROLOGY

The climate of Hong Kong is subtropical, winters cool (a mean minimum of 13.2°C in January) and dry (a mean minimum of 26.9 mm precipitation in January), summers hot (a mean maximum of 31.6°C in July) and wet (a mean maximum of 431.8 mm in June).

Geomorphologically, Hong Kong comprises an eroded mountain chain of metamorphosed sedimentary rocks with granitic and volcanic intrusions. Following the last ice age, sea water levels have risen by some 10 m, so that former river valleys and lowland areas are now drowned. The numerous offshore islands represent former mountain tops. The majority of Hong Kong is, therefore, of steep bedrock covered by a thin layer of top soil. To the northwest, however, Hong Kong abuts the delta and flanks the western mouth of the Pearl River, the largest river of southern China, draining an area of some 228,000 km^2 and with an annual flow of 308 billion m^3. Because of the climate, over 80% of this discharge occurs in summer. This area of Hong Kong comprises flat alluvial plains, with numerous rivers, all tributaries of the Pearl, creating extensive estuarine flats, bordered by mangroves and marshlands. Within the Pearl River delta, therefore, is the potential for wide habitat segregation, but this is not generally true of Hong Kong itself.

Because of the land's steep slopes, surface runoff is rapid, a situation which has been exaggerated by extensive diversion of stream and river waters into catchments to supply potable water for Hong Kong's expanding population of around 6 million.

Streams are therefore "flashy". Many dry up in winter and flood in summer following torrential rains, especially after a typhoon. A biological side benefit of potable water supply has been the construction of large lakes as reservoirs. The first of these, Plover Cove, was completed in 1967. It was created by damming a 14 km^2 tidal inlet and formed Hong Kong's first "reservoir in the sea". The second, High Island, was completed in 1979 and built by damming an area of sea separating a large island from the mainland. Hitherto, because of geomorphology, Hong Kong had no natural lakes and only small, winter drained, reservoirs. A number of bivalves, i.e. *Anodonta woodiana* (Lea), *Corbicula fluminea* (Müller) and *Limnoperna fortunei* (Dunker), have been introduced into Plover Cove and High Island.

Agricultural practices have also modified the freshwater environment by widescale diversion of lowland streams into flooded vegetable gardens. This has created shallow, semipermanent, artificially managed, nutrient enriched, slow-flowing watercourses. Of late, however, because of extensive development for urban renewal, these habitats are disappearing, reconforming the environment.

The diversity, species composition and relative abundance of Hong Kong's fresh and brackish water bivalve fauna thus results from and is dependent upon the changing influences of climate, geomorphology, and human modification. A greater variety of species occurs in the surrounding lands and waters of China, but how Hong Kong's discrete bivalve fauna is adapted to this dynamic environment, exposes underlying principles.

SYSTEMATICS

Table 1 lists the species of fresh and brackish water bivalves recorded from southern China (Guangdong Province). Excluded from this list are a number of brackish water mangrove-associated bivalves which have clear phylogenetic affinities with marine families. Thus, *Polymesoda (Geloina) erosa* (Solander) (Corbiculidae) is included because it exclusively occurs around fresh water seeps draining through high, upper zone, mangroves. Conversely, the low zoned, mangrove associate, *Gafrarium pectinatum* (Linnaeus) (Veneridae), is excluded. Similarly the wholly and uniquely fresh water mytilid *Limnoperna fortunei* is included, but the brackish water mangrove associate, *Brachidontes variablis* (Krauss) is excluded because of a much wider local distribution on many kinds of shores (Lee and Morton, 1985).

Taxonomic problems have surrounded a number of these species, notably *Anodonta woodiana* (Unionacea), *Polymesoda (Geloina) erosa* (Corbiculacea) and *Corbicula fluminalis* (Müller) and *C. fluminea* (Corbiculacea). In the case of *Anodonta woodiana*, Brandt (1980) first reported *Cristaria (Pletholophus) discoidea* (Lea) and *A. gibba* Clessin from Hong Kong and Dudgeon (1980b) described some aspects of the biology of the former species. It is now known (Dudgeon and Morton, 1983; 1984) that both of these names actually refer to *A. woodiana*. This species is widely distributed in China, has been introduced into Indonesia (Djajasasmita, 1982) and has a variable shell form, so much so that Liu *et al.* (1979) record it as comprising four subspecies. Species of *Polymesoda* are difficult to differentiate, though this has been undertaken by Morton (1984) and only *P. erosa* has been recorded from mainland China, although two other species are reported from mangroves elsewhere in Asia.

Greatest taxonomic problems reside with the Asian species of *Corbicula*. An array of species has been described, but Morton (1979a; 1986a) considers that these can all be ascribed to two, i.e. *Corbicula fluminalis* and the highly variable *C. fluminea*. The latter has been introduced into N. America, Europe and Argentina (Britton and Morton, 1979, 1982, 1986; Morton, 1986a). The problems lie in the fact that *C. fluminea*, at least, is polymorphic with respect to shell form, colour and expression of sexuality (Britton and Morton, 1986; Morton, in prep.). Two distinct colour morphs occur in the American southwest, one straw-coloured, the other dark

Table 1. The fresh and brackish water bivalves recorded from Hong Kong and the southern Chinese Province of Guangdong.

	Southern China	Hong Kong
Mytilacea		
Limnoperna fortunei (Dunker)	+	+
Unionacea		
Union douglasiae (Gray)*	+	—
Lamprotula leai (Gray)*	+	—
Anodonta woodiana (Lea)	+	+
Corbiculacea		
Polymesoda (Geloina) erosa (Solander)	+	+
Batissa (Cyrenobatissa) subsulcata Clessin	+	—
Corbicula fluminalis (Müller)	+	—
Corbicula fluminea (Müller)	+	+
Musculium lacustre (Müller)	+	+
Pisidium clarkeanum G. and H. Nevill	?	+
Pisidium annandalei Prashad	?	+

*Information obtained from Liu *et al.* (1979)

(Fontanier, 1982; Hillis and Patton, 1982; Britton and Morton, 1986). The same is true of Hong Kong, though the discovery of an intermediate morph establishes a high degree of phenotypic plasticity for this species related to variations in hydrology and thus occupation of a heterogeneous environment (Morton, in prep.).

LIFE HISTORY TACTICS AND SEXUAL STRATEGIES

Anodonta woodiana probably did not occur in Hong Kong prior to the development of larger permanent reservoirs. The construction of Plover Cove in 1967, with colonisation by a range of organisms commencing in 1968 (Morton, 1977a, b), has permitted the establishment of a population of *A. woodiana* that survives as glochidial larvae on fish fins, even if the parent population is largely killed off in winter as a result of drawdown. A study of *A. woodiana* by Dudgeon and Morton (1983), showed that individuals probably live (in Hong Kong) to a maximum age of 12 years. In Plover Cove, the species is dioecious with females predominating in a ratio of 3:2. A small number of individuals (0.3%) are hermaphrodites. Males possess mature gonads throughout the year, whereas females come into reproductive condition during the spring. Eggs are produced throughout the summer and are brooded in the outer demibranchs of the ctenidia. In any one year there is a single phase of recruitment in summer, glochidia residing for a mean time of 14.4 days on the host at 15°C but only 6 days at 27°C (Dudgeon and Morton, 1984).

Polymesoda (Geloina) erosa is restricted to mangrove stands in east Asia (Morton, 1984) and shows remarkable physiological adaptations to a high-zoned life in this habitat. These include pedal gape feeding on subterranean waters, aerial respiration and an ability to tolerate extended periods of desiccation (Morton, 1975b; 1976; Depledge, 1985). The species typically inhabits streams or seeps draining through the mangal and is covered by most tides, if for only a short time. Thus, despite habitation of a "difficult" environment, it is tidally "predictable", and the species has evolved a range of behavioural and physiological adaptations suited to it. Sexually, however, *P. erosa* is unspecialized. Each individual is dioecious though, as with *A. woodiana,* a greater percentage of individuals are females (i.e. 51.5%, with 38.5% male and 9.5% immature) (Morton, 1985a). *P. erosa* does not incubate fertilized eggs in the ctenidia. Age analysis is difficult because of considerable acid mangal erosion of the shell, but individuals clearly live longer than one or two years.

Batissa (Cyrenobatissa) subsulcata Clessin is a large corbiculid occurring in the Pearl River system and occasionally found for sale in Hong Kong markets. There are no references to this species in the Chinese literature but Dudgeon (1980a) obtained a small commercial sample and undertook simple analysis of it. The largest specimen was 73 mm long and had 9 growth rings. Construction of a Walford plot (Walford, 1946) showed that a maximum theoretical length of 77 mm was possible. Such individuals might be expected to have 11 growth rings. Nothing is known of the life history or reproductive strategies of this species, but assuming there is either one or two periods of reproductive activity each year then clearly a life span of either 11 or 5.5 years is theoretically possible.

The mangrove associated *Polymesoda erosa* and the riverine *Corbicula fluminalis* are both dioecious, oviparous and breed but once a year. In view of the close taxonomic relationship and obvious anatomical similarities between these three corbiculids, I speculate that *Batissa subsulcata* can be likewise dioecious, nonbrooding, with a single cycle of gametogenesis each year and living for a maximum of approximately 11 years.

A freshwater mytilid has been recorded from wide areas of China. Most Chinese authors, i.e. Tchang *et al.* (1965), Chen (1979) and Liu *et al.* (1979), refer to this as *Limnoperna lacustris* Martens, which Habe (1977) synonymises with *L. fortunei.* Mizuno and Mori (1970) record *L. fortunei* from Thailand while Brandt (1974) records *L. supoti* Brandt from Thailand, and Brandt and Temcharoen (1971) record *L. depressa* Brandt as new from Laos and Cambodia. Morton (1973, 1975a, 1977b, 1982b) refers to *L. fortunei* from Hong Kong. The species is known to occur in the headwaters of the Pearl River around Guangzhou (Canton) (Miller and McClure, 1931). It has been introduced from this region, in potable water supplies, to Hong Kong where it now occurs in Plover Cove Reservoir (Morton, 1975a) and in pipelines both to and from the reservoir. It has not, however, spread into natural watercourses. In southern China therefore the species normally occupies more permanent, predictable, lentic and lotic habitats but not natural streams and temporary watercourses. Throughout its wide range, however, the species, has been attributed with much opportunism

(Morton, 1973; 1975a, 1977b).

Although *Limnoperna fortunei* has been recorded from brackish waters (Miller and McClure, 1931) it has also colonised Plover Cove following the advent of stable conditions therein (Morton, 1977b). The species is dioecious, 65.7% of the population being female. No hermaphrodites were found in a sample of 291 individuals examined by Morton (1982b). Eggs are fertilized externally and settlement occurs twice a year in summer (June-August) and winter (November-December), when air and water temperatures are approaching maxima and minima, respectively. The species is estimated to live for two or three years (Morton, 1977b).

Corbicula fluminalis occurs in the Pearl River estuary, but no information is available on its salinity tolerance. An analysis of population structure in this species by Morton (1982a) has shown that a maximum theoretical length of 64 mm is possible in the Pearl River and that the life span may be up to 10 years. A single growth ring is produced each year. Breeding occurs once a year in winter.

An analysis of 656 individuals over a 20 month period has shown that 49.7% of the population were female, 45.7% male, and 4.5% hermaphrodite. However, a greater percentage of smaller, younger, individuals were female (59.2%) and larger, older, individuals were predominately male (58.5%). Morton (1982a) interpreted this as a trend towards protogyny and as an aspect of an overall strategy, along with the low incidence of hermaphroditism, towards enhancing the options available for reproductive success in a large lotic environment. No evidence of ctenidial brooding of fertilized eggs was found but, strangely, glands which in *Corbicula fluminea* develop in the inner demibranch only when larvae are being brooded, also developed in younger specimens of *C. fluminalis*. The question was posed by Morton (1982a): does *C. fluminalis* have variable sexual strategies over different components of its range?

Evidence for such variability is not available for *Corbicula fluminalis*, but is accumulating for a close relative, *C. fluminea*. This species is widespread in China with an enormous natural distribution plus an introduced distribution in North America, Europe and South America (Morton, 1986a). Many species names describe it, but it has a highly variable shell form, colour and maximum size and can osmoregulate in salinities up to 13% (Morton and Tong, 1985). It is, moreover, characterized by great variability in life history traits and sexual strategies. *C. fluminea* lives for between 3 - 4 years, with two peaks of larval production typically in spring and autumn. Fertilized eggs are brooded in the inner demibranchs to a larval shell length of some 220 μm. Individuals can be dioecious or hermaphroditic (Kraemer, 1979). Reproductive strategy is very variable. Morton (1983) showed that in a lentic habitat (Plover Cove), the population comprised approximately equal proportions of males, females and hermaphrodites. In an agricultural flooded furrow, however, the population comprised approximately equal numbers of females and hermaphrodites only. A variable expression of sexuality in this dimension is relatively easy to understand, but the most recent researchers by Britton and Morton (1986) and Morton (in prep.) on this species in North America and Hong Kong, respectively, have shown it to be highly polymorphic with respect to shell form, colour and sexual expression. Two form extremes are defined as A and B. A form individuals are typically straw-coloured with widely spaced concentric lamellae and are predominately female (i.e. 73% female vs. 25% hermaphrodite). B form individuals have dark shells as the result of progressive enlargement and fusion of umbonal colour flashes seen in all juveniles. Concentric lamellae are narrowly spaced and these morphs are predominately hermaphroditic (75% hermaphrodite vs. 18% female). The two morphs may be sympatric or allopatric, this being determined by inter- and intra-stream variations in water quality, notably with regard to hardness for shell form and potassium (in combination with pH, dissolved oxygen and carbon dioxide) for colour and the expression of sexuality (Morton, in prep.).

Hillis and Patton (1982) consider these morphs to be distinct species on the evidence of fixed homozygous allelic differences at 6 of 26 genetic loci; nevertheless, Morton (in prep.) has identified a morph intermediate in shell colour between A and B, and believes all morphs to be expressions of a single genotypically variable and phenotypically plastic species.

The holarctic species, *Musculium lacustre* (Müller), has been studied elsewhere (Mitropolskji, 1965; Mackie, 1978b; 1979; Mackie and Huggins, 1983). In Hong Kong it occurs in agricultural drainage ditches and has been shown by Morton (1985b) to be a simultaneous hermaphrodite, but with evidence that the testis matures first. Maturity is attained at a shell length of 2 mm, though the majority of individuals are brooding larvae within marsupia of the inner demibranchs at a length of between 4 - 6 mm. The larvae are released at a length of 1.5 mm and, growing rapidly, quickly mature to contribute to a succeeding generation. Thus, although recruitment occurs in two major peaks each year, in spring and autumn, this is not because of iteroparity, but represents life cycle completion by two overlapping generations. The spring recruits give birth to the fall recruits which in turn give birth to the succeeding spring recruits. *M. lacustre* is thus generally semelparous and univoltine. A few of the late-born spring generation can, however, overwinter to contribute to the spring generation of the succeeding year. These animals would thus be iteroparous and bivoltine. This is not so with the fall generation and a life span estimate of between either 6 (autumn generation) or 12 (spring generation) months seems appropriate for this species in Hong Kong.

Pisidium clarkeanum G. and H. Nevill and *P. annandalei* Prashad are sympatric in the flooded furrows of vegetable gardens in Hong Kong's New Territories and have been studied by Morton (1986b). The former species attains a maximum length of 7.0 mm, the latter 4.0 mm. Both are simultaneous hermaphrodites and ovoviviparous. *P. clarkeanum* is sexually mature at a shell length of 2.0 mm and *P. annandalei* at 1.5 mm, though larvae are not brooded in the former until a length of 3.0 mm is attained and in the latter at 2.0 mm. Larvae are released at a length of 1.2 mm in *P. clarkeanum* and 0.8 in *P. annandalei*.

Three generations are produced each year by both species, but since these represent single recruitments from the preceeding generation, both species are basically semelparous and univoltine. Because of an overall greater longevity, *Pisidium clarkeanum* can, however, following one birth period, produce a second generation to contribute to the succeeding generation and is thus iteroparous and bivoltine. This strategy is unlikely in *P. annandalei* and rarely, if ever, can individuals be iteroparous. Maximal life span estimates for these two species are thus 8 months (*P. clarkeanum*) and 4 months (*P. annandalei*).

Life history traits and sexual strategies of the Hong Kong species of fresh and brackish water bivalves are summarised in Table 2. There seems to be a division of the species into three categories. There are those species occupying large, permanent, water masses, i.e. either lakes or rivers, which can be defined as predictable habitats influenced only by major climatic changes. Here the species are generally large, have an enhanced longevity of >10 years and are characteristically dioecious (though small percentages of all are hermaphroditic) and iteroparous. Unlike the other species characterizing this category, *Anodonta woodiana* is a confirmed brooder, but this can be explained by the highly specialised method of dispersal, uniquely adopted by representatives of the Unionacea, a glochidia larva attaching to fish fins (Dudgeon and Morton, 1984). Generally, with this one exception, these bivalves are non-brooders and can all be defined as K-selected species.

A second category of bivalves includes but two species, i.e. *Limnoperna fortunei* and *Corbicula fluminea*. These bivalves are also iteroparous, with life spans of between 2 - 4 years. A shell length of some 30 - 40 mm is common. In terms of sexual strategies, however, the two are different. *L. fortunei* is dioecious (with no hermaphrodites), and *C. fluminea* has a wide range of sexual expressions, but with larval brooding. These can best be defined as r-selected species adapted to the invasive colonisation of a wide range of aquatic environments. There is strong evidence that both species have entered fresh waters relatively recently. Reduced life spans, ages of maturity and the retention of an invasive planktonic juvenile dispersal stage in the case of *L. fortunei* or of internal fertilization but release of large numbers of shelled larvae in the case of *C. fluminea* facilitate such opportunism.

In contrast to the classical examples of K- and r-selected categories of species defined above, there are three species of pisidiid bivalves found in Hong Kong, i.e. *Musculium lacustre, Pisidium clarkeanum* and *P. annandalei*, which are more difficult to categorise. These species are all

Table 2. The life history tactics and sexual strategies of the fresh and brackish water bivalves of Hong Kong and southern China.

	Species	Sexual expression	Semelparous/ iteroparous	Brooding	Recruitment periods/year	Life span	Authority
K-selected species of large permanent lotic or lentic habitats	*Anodonta woodiana*	Dioecious	Iteroparous	Outer demibranch	Once (Spring)	12 years	Dudgeon and Morton, 1983, 1984
	Corbicula cf. *fluminalis*	Dioecious with a trend towards protogyny	Iteroparous	Not	Once (Winter)	10 years	Morton, 1982a
	Polymesoda (Geloina) erosa	Dioecious	Iteroparous	Not	Once (Summer)	>8 years	Morton, 1985a; Morton (unpublished data)
	Batissa (Cyrenobatissa) subsulcata	Dioecious	Probably iteroparous	?	?	10-11 years	Dudgeon, 1980a; Morton (unpublished data)
r-selected species of lotic and lentic habitats with unpredictable perturbations	*Limnoperna fortunei*	Dioecious	Iteroparous	Not	Twice (Spring & Autumn)	2-3 years	Morton, 1977b, 1982b
	Corbicula fluminea	Dioecious/ hermaphrodite	Iteroparous	Inner demibranch	Twice (Spring & Autumn	3-4 years	Morton, 1977a, 1983
K-selected species of small lentic habitats with predictable perturbations	*Musculium lacustre*	Simultaneous hermaphrodite	Generally semelparous	Inner demibranch	Twice (Spring & Autumn	6-12 months	Morton, 1985b
	Pisidium clarkeanum	Simultaneous hermaphrodite	Generally semelparous	Inner demibranch	Three	4-8 months	Morton, 1986b
	Pisidium annandalei	Simultaneous hermaphrodite	Generally semelparous	Inner demibranch	Three	4 months	Morton, 1986b

short-lived, i.e. less than 1 year, attain a shell length of less than 10 mm, and are generally semelparous, with the possibility (only) of iteroparity. They all brood few larvae in highly specialized ctenidial marsupia and are exclusively hermaphroditic. Two or three overlapping generations are produced each year. The above adaptations suit these species to life in small artificially lotic habitats which in Hong Kong experience predictable perturbations, particularly in terms of seasonal variations of wetting and drying. These species are physiologically and reproductively adapted to such predictable seasonal events, just as the K-selected large lentic and lotic species are adapted to predictable winter reductions in ambient temperature. In such a case therefore, Hong Kong's pisidiid species should also be categorized as K-selected species, albeit with reproductive strategies and life history tactics which are completely different from their relatives inhabiting larger water bodies (Table 3).

DISCUSSION

This study is concerned with defining the different reproductive strategies and life history tactics adopted by various species of fresh and brackish water bivalves from southern China.

The environmental predictability associated with lentic and lotic water bodies of larger scale is clearly reflected in their bivalve inhabitants by enhanced longevity, gonochorism, external fertilization and non-brooding, all K-selected features. Conversely, pisidiid inhabitants of small lentic habitats, either of shorter (seasonal) or long term scale, are characteristically small, short-lived (less than 1 year), typically hermaphroditic, semelparous and brood but a few larvae within highly specialised ctenidial marsupia. These too can be considered as K-selected traits albeit occurring in species occupying what are usually considered to be r-variable habitats.

Between these two groups of species in Hong Kong are two bivalves one of which, at least, gives a different insight into the adaptations that allow species to transgress important ecological boundaries. Much of this discussion will relate to *Corbicula fluminea*, but in some ways *Limnoperna fortunei* is similar, i.e. both can occur in lentic and lotic situations and both live for 2 - 3 years. Less detail is known of *L. fortunei*, however, and which, unlike *C. fluminea*, is dioecious and non-brooding (Morton, 1982b).

Corbicula fluminea occupies a wide range of habitats throughout its natural range (which includes Hong Kong) and in its introduced range in North America. Lakes, rivers, streams, ponds, ditches and drains are equally favoured. A picture is emerging of a species with wide variations in shell form and colour (polymorphism) and, most important, wide variations in sexual expression. *C. fluminea* can be either dioecious or hermaphroditic, and different populations comprise such individuals in different ratios. Schaffer (1974) argued that populations which live in unpredictable environments should be polymorphic for reproductive characteristics, and Giesel (1974) demonstrated that polymorphic populations were more fit (in terms of average rate of increase and total population size after 300 reproductive intervals) than were monomorphic ones. Generally these principles and characteristics of r-selected species have been applied to pisidiid bivalves producing many young and occupying a wide range of unpredictable habitats (Heard, 1977). However, other pisidiids are K-strategists, occupying more stable habitats and producing few offspring, as with the Hong Kong species (Morton, 1985b, 1986b).

For the Pisidiidae, however, important inter-population differences in sexual strategies (but not sexual expression) have been documented and have been reviewed by Burky (1983). In either temporary ponds or perennial habitats, *Musculium securis* (Prime) is respectively iteroparous or semelparous (Mackie, 1978b; McKee and Mackie, 1981). Mackie and Flippance (1983) have shown that in a big pond *Sphaerium rhomboideum* (Say) has one birth peak a year, lives for longer than 14 months, and is iteroparous. In a small, temporary pond, the same species has 3 birth peaks, a faster average summer growth rate, a shorter life span, is either semelparous or iteroparous and suffers less mortality. Holopainen (1979) has shown that littoral populations of *Pisidium*

Table 3. The generalised life history tactics and sexual strategies of fresh and brackish water bivalves occupying habitats characterised by different degrees of predictability in southern China and Hong Kong.

	Habitat range	Habitat type	Longevity (years)	Semelparous /iteroparous	Recruitment periods/ annum	Sexual expression	Extent of parental brooding
1. K-selected species	Narrow	Perennially predictable:	>10	Iteroparous	1	Dioecious (females predominating; a few hermaphrodites	External fertilization (Oviparous)*
2. r-selected species	Wide	Perennial/ ephemeral	Intermediate 2-4	Iteroparous	2	Mixed: Dioecious/ hermaphrodites	Oviparous/ ovoviviparous
3. K-selected species	Narrow	Seasonally predictable:	<1	Semelparous	>2	Hermaphrodites	Ovoviviparous

*the exception is *Anodonta woodiana*

casertanum (Poli) produce one larval litter per year, but that profundal populations of the same species have two litters per year.

Such modifications in the Pisidiidae, however, relate to interpopulation variations in longevity, rates of growth, reproductive timing, larval growth rates and relative rates of adult vs. larval mortality and can be regarded as variations in life history traits permitting colonization of a range of seasonally fluctuating or short lifespan microhabitats. Intraspecific comparisons of pisidiid populations, moreover, point out that if juvenile mortality is more variable than adult mortality then the stochastic bet-hedging theory of Stearns (1976; 1977) may be more applicable than any categorisation into r- and K- (Hornbach *et al.*, 1980b; Way *et al.*, 1980; McLeod *et al.*, 1981). One could argue that the mix of sexual expressions adopted by inhabitants of predictable habitats, e.g. *Corbicula fluminalis* (Morton, 1982a) with a small percentage of hermaphrodites in an otherwise dioecious population is another expression of the mixed tactic theory. Such a strategy would also be typical of *Anodonta woodiana* (Dudgeon and Morton, 1983) and *Margaritifera margaritifera* (Linnaeus) (Smith, 1979).

Of much greater significance resulting from (but perhaps also permitting) colonization of a far wider range of habitats are the polymorphisms in shell form, colour and sexual expression adopted by *Corbicula fluminea.* Species of *Sphaerium, Musculium* and *Pisidium* are readily identifiable, the affinity of species based on morphology being consistent with the general size and shape of the shells of the species studied (Hornbach *et al.*, 1980a), and always simultaneous hermaphrodites (Mackie, 1978a). This is not so with *C. fluminea.* Shell form and colour vary to such an extent that literally hundreds of species names have been ascribed to it (Morton, 1979a); and sexual expression varies between lotic and lentic populations and even within sub-populations inhabiting different branches of the same streams. In such cases, a subtly different hydrology is believed responsible for observed variations in morph ratios.

It is well known that molluscan shell form and colour are genotypically determined and phenotypically plastic. For a review of this subject see Berger (1983). The best example is of *Mytilus galloprovincialis* Lamarck regarded by some as a separate species from *M. edulis*, (e.g. Wilkins *et al.*, 1983), but as a subspecies or ecomorph by others, (e.g. Gosling, 1984). Such "species" are genotypically variable and phenotypically plastic and the term "opportunistic" has often been applied to them. Exhibiting a wide range of form, such species are apparently successful in an equally wide range of habitats. This is particularly true of some freshwater bivalves, notably byssally attached species which move into a wide variety of microhabitats after having been introduced into areas outside their natural range. The Dreissenacea offer the best examples, i.e. *Dreissena polymorpha* Pallas in Europe (Morton, 1979b) and *Mytilopsis sallei* (Recluz) (Morton, 1981) in Asia. Although studies upon these bivalves are few, it is known that each genus contains highly variable species. Zahdin (1965), for example, considers there to be 7 species of *Dreissena* in the U.S.S.R., all determined by subjective character analysis. Nine species of *Mytilopsis* are supposedly extant, but with 66 synonyms. Marelli and Gray (1983) redescribe *M. sallei* (Recluz) and *M. leucophaeta* (Conrad) on shell characters alone, but note the original descriptions can easily apply to specimens of any species of the genus. As noted earlier, new species of *Limnoperna* are being erected (Brandt and Temcharoen, 1971). Where objective analysis has been applied to shell characters, e.g. *Corbicula fluminea* (Britton and Morton, 1986), "species" differentiation has not been possible. The proliferation of species names for *Dreissena, Mytilopsis, Corbicula* and *Limnoperna* therefore seem to this author to probably reflect no more than high genotypic variability and phenotypically plastic character traits which mark highly opportunistic (r-selected) and recent colonists of the freshwater domain.

Most studies of freshwater bivalves have concerned themselves with the Unionacea and Pisidiidae, which are phylogenetically old residents of freshwater systems and therefore highly specialised both physiologically and reproductively and in terms of life history traits.

This study of a discrete guild of southern Chinese bivalves, however, exposes and draws attention to the importance of another category of opportunistic species in studies of freshwater ecology.

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A NEW MONTE CARLO METHOD FOR ASSESSING TAXONOMIC SIMILARITY WITHIN FAUNAL SAMPLES: REANALYSIS OF THE GASTROPOD COMMUNITY OF ONEIDA LAKE, NEW YORK

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ABSTRACT

Using frequency table analysis and log-linear models, Dillon (1981) concluded that bottom samples taken by F. C. Baker (1918) from Oneida Lake, New York, had significantly fewer pairs of confamilial snail species than expectation based on a Monte Carlo simulation unweighted by relative abundance. If confamilial species are assumed to have similar ecological requirements, these findings suggest that competition has played a role in determining the micro-distribution of snails in Oneida Lake. However, the statistical tests employed in 1981 were weak in many respects. So in this study, I propose a new method of assessing the taxonomic similarity within faunal samples to re-examine F. C. Baker's data. Samples are categorized simultaneously by the number of species and the number of higher taxa they contain using a tabular format, and the resulting distribution of samples by species is used in a Monte Carlo simulation. Results were similar to those of 1981. The taxonomic similarity of snail samples cannot be distinguished from random expectation based on an abundance-weighted model. But if species are assumed to have equal chances of occurring in samples, regardless of their relative abundances, samples from Oneida Lake tend to have substantially fewer genera and families than expected.

The similarity of co-occurring animals has been the object of considerable study and debate for about 40 years. The extensive literature has recently been reviewed by Harvey *et al.* (1983) and by Strong *et al.* (1983). In general, it has been established that a relationship exists between an organism's diet and its morphology. The more similar a pair of organisms are morphologically, the more likely it is that they will rely on similar resources. Thus early workers (Elton, 1946; Hutchinson, 1959) expected that co-occurring animals ought to be unusually dissimilar morphologically in order to reduce competition. Others (e.g. Simberloff, 1970) have suggested the opposite, that co-occurring animals may tend to be unusually similar, since similar animals have similar dispersal capabilities and similar ecological needs. Much debate has centered upon the statistical tests that can be appropriate to distinguish these two alternatives from a third, that no pattern exists at all regarding species similarities and distributions.

Two general methods have been used to estimate overall morphological similarity. The more direct approach involves measuring the size and shape of various anatomical features on representative specimens from each taxon being studied (Strong *et al.*, 1979; Simberloff and Boecklen, 1981; Bowers and Brown, 1982; Case *et al.*, 1983; Travis and Ricklefs, 1983; Schum, 1984). Difficulties arise, however, in the selection of relevant characters to measure and appropriate individuals to measure them on. This latter problem is particularly acute in species (e.g. most mollusks) where there is no discrete adult size. Thus there are attractions to the use of taxonomic "relatedness" as a measure of morphological similarity (Elton, 1946; Williams, 1947; Simberloff, 1970). Here it is assumed that species in the same genus, for example, are very similar to each other. But species in different genera of the same family are somewhat less similar, the species of different families are less similar still, and so on. Data of this sort are very easy to obtain, but are somewhat difficult to analyse.

Dillon (1981) used both morphometric and taxonomic methods to estimate the similarity of snails co-occuring in small samples taken from the bottom of Oneida Lake, New York, by Baker (1918). Taxonomic similarity was estimated using the number of congeneric and confamilial pairs of species. Then the observed taxonomic similarities were compared to those expected from Monte Carlo simulations using frequency table analysis. But this method was weak in several respects. Because it was based on chi-square statistics, a great deal of data-pooling was necessary to obtain the minimum sample sizes required in each cell. Congeneric triplets and quadruplets were difficult to handle. And further, the contribution of any particular factor to the fit eventually obtained between actual data and log-linear model cannot be assessed independently of other effects in frequency table. A number of indirect tests suggested, however, that some differences between the taxonomic similarity observed in Baker's data and that expected from simulations were substantial.

Here I describe a new test to analyse taxonomic similarity within faunal samples that avoids the difficulties outlined above. Instead of counting congeneric or confamilial pairs, entire distributions of genera or families are compared. I will use this new technique to reanalyse Baker's data on the distribution of gastropods in Oneida Lake.

METHODS

Details regarding the collection of the data to be analysed here can be obtained in Baker (1918). Briefly, Baker made 162 quantitative samples of plants and macrobenthos, primarily using a long-handled dipper or a dredge. Twenty-one of these samples either contained no snails or were omitted from the report. Collected in the remaining 141 samples were 5,716 individual snails, representing 37 species and subspecies. Omitting very rare species and lumping those that have been synonymized, Dillon (1981) reduced these numbers to 5,582 individuals representing 23 species. The species involved, their distributions and abundances, and the higher systematic categories recognized are all given in Dillon (1981).

The 121 samples with more than one species present were first categorized simultaneously by the number of species and genera they contained. This was most conveniently accomplished using a data table with the number of species listed down the left margin and the number of genera listed across the top. Then the number of samples containing two species, three species, and so forth, was totalled down the right-hand margin of the table. The total number of samples containing one genus, two genera, and so forth, was totalled at the bottom. Distributions of samples by the number of species and higher taxa they contained will be referred to as S distributions and T_0 distributions (higher taxa observed), respectively. Table 1 illustrates this technique. An identical procedure was also used to tabulate the samples by the number of families they contained.

If there is no tendency for co-occurring snails to be more or less similar to one another taxonomically, a random sample of species from the Oneida Lake fauna using the S distribution should give a distribution of genera or families (T_e, higher taxa expected) indistinguishable from T_0. But if co-occurring snails tend to be taxonomically dissimilar, for example, the T_0 distribution will tend to be higher than the randomly-generated T_e distribution. Just as in the 1981 analysis, T_e distributions were obtained using two algorithms.

Table 1. Baker's (1918) samples from Oneida Lake, New York, categorized by the number of species and genera of snails they contained. The row totals constitute the S distribution, and the column totals the T_0 distribution.

		NUMBER OF GENERA								
		1	2	3	4	5	6	7	8	T
	2		27							27
	3			23						23
	4			2	19					21
	5			1	4	22				27
Number of Species	6				1	1	7			9
	7				1	1	3	4		9
	8						1			1
	9						1	1	1	3
	10						1			1
	T	0	27	26	25	24	13	5	1	121

For the abundance-weighted test, a pool was created in which each snail species was represented according to its abundance over all 141 samples taken. For example, Baker collected a total of 17 *Campeloma decisum* (Say) in his 141 samples, so the probability of selecting *C. decisum* from the species pool was 17/5,582 = 0.003. Notice that data from samples containing only one species are included in the calculation of relative abundances, although not in the compilation of the S distribution. Then a uniform random number generator was used to draw "samples" from the species pool, with replacement, following the S distribution. The number of random samples taken was 100 times the number of actual observations. For example, Table 1 shows that the S distribution has 27 samples with two species represented, 23 samples with three species, and so on, up to one sample with ten species. Thus in the computer simulation, 2700 samples were taken including two different species from the species pool, 2300 samples were taken of three different species, and so on, up to 100 samples of ten species. These randomly-generated samples, categorized by the number of genera of families they contained, constituted the two T_e distributions. Table 2 illustrates this method and shows the results from the analysis of genera.

Techniques were quite similar for the abundance-unweighted simulation, the only difference being that all 23 species had equal probabilities of being selected from the pool. Thus the probability of drawing *Campeloma decisum* was 1/23 = 0.043. The two T_e distributions, one for genera and the other for families, were generated by drawing 100 times the S distribution as before. Copies of the computer program (in Basic) used for the generation of both weighted and unweighted T_e distributions are available from the author.

The T_0 and T_e distributions were compared using values of the Kolmogorov-Smirnov statistic D from one-sample tests (Siegel 1956: 47). The D statistic is the maximum difference between the cumulative expected distribution and the cumulative distribution actually observed. Normally, D statistics are presented as absolute values. But for this application, a positive value of D will indicate that T_0 distributions tend to take higher values than T_e, and therefore that co-occurring snails tend to be taxonomically dissimilar. A negative value of D will suggest the opposite. It should be cautioned that D-statistics are sensitive to any sort of deviation from expectation, not just difference in central tendency.

Table 2. Results of the Monte Carlo simulation of Baker's (1918) samples from Oneida Lake. The row totals are the S distribution, and the column totals the T_e distribution of genera.

		NUMBER OF GENERA									
		1	2	3	4	5	6	7	8	9	T
	2	44	2656								2700
	3		154	2146							2300
	4		1	328	1771						2100
Number of Species	5			40	797	1863					2700
	6				43	377	480				900
	7				3	124	476	297			900
	8					2	26	51	21		100
	9						32	120	122	26	300
	10						2	23	54	21	100
	T	44	2811	2514	2614	2366	1016	491	197	47	12100

Thus the data were always plotted and examined critically before any conclusions were drawn from the D-statistics.

Ideally, one would want to know the likelihood that a T_o distribution might arise as a random sample from a given T_e distribution. The unusual composition of T distributions, however, precludes inference regarding the significance of D or any other conventional statistic. Although T distributions can theoretically take any frequency from 0.0 to 1.0 at the lower end of the scale, frequencies are constrained at values above 2 higher taxa present. Because no more than two higher taxa can be present when only two species are present, and no more than three higher taxa can be present in samples of three species, and so forth, T distributions are not completely free to vary at the upper end of their ranges. Thus it seems possible that T_o distributions would be more likely to underestimate than overestimate T_e distributions. That is, this technique would seem to be biased towards finding that co-occurring animals seem to be more similar than random expectation.

In order to investigate the strength of this and other potential biases, Dillon and Schotland (unpublished data) used this technique to analyse a large series of randomly-generated data sets. We found substantial bias only under very extreme conditions. In the normal range of species abundances and aggregations, there is little detectable difference between T_o and T_e. So although I can present no confidence estimates with the results of my analysis, simple inspection of D statistics and graphed results should give a reasonably reliable indication of trends in taxonomic similarity.

RESULTS

The four comparisons between observed and expected taxonomic similarity are plotted in Figure 1. The observed data seem to fit abundance-weighted expectation fairly well. Values of D are 0.017 for the genus comparison and -0.083 for the family comparison. As a yardstick, the critical value of D from a one-sample K-S test with $N = 121$ is 0.123 (two-tailed). Thus the probability that gastropod species co-occur in Oneida Lake would seem to be a function of relative abundances but not taxonomy. There is no evidence that congeneric or confamilial species have significant tendencies to occur together or to occur apart, assuming the abundance-weighted hypothesis.

On the other hand, both T_o distributions seem to be shifted substantially to the right of T_e distributions based on abundance-unweighted simulations. The values of D are 0.107 for the genus comparison and 0.099 for the family comparison. Given the sample size of 121, these values are as large or larger than the most extreme values of D generated in the simulation tests of Dillon and Schotland. Thus there is fairly good evidence that snails co-occurring in samples taken from the bottom of Oneida Lake tend to be more dissimilar taxonomically than random expectation unweighted by species abundance.

DISCUSSION

Although derived using a different technique, these results agree well with those of Dillon (1981). The earlier analysis also suggested that the taxonomic similarity of co-occurring snails seems to be indistinguishable from random expectation if the probability of occurrence for each species is weighted by its abundance. But if all species are equally likely to occur, it appears from both analyses that co-occurring snails tend to be taxonomically dissimilar.

Unweighted Monte Carlo simulations would initially seem to be less realistic and thus less interesting to test than the abundance-weighted ones. But if relative abundances are viewed as a function of recent environmental conditions and the life cycles of the species involved, these abundances can change rapidly. Thus abundance-unweighted "null hypotheses" have been more commonly tested by previous researchers.

Dillon (1981) examined the morphometric similarity of co-occurring gastropods as well as their taxonomic similarity. Judging from size and shape of the shell and radula, it was concluded that snail species co-occurring in Oneida Lake tend to be significantly more dissimilar than the abundance-weighted simulation would suggest. Considered along with the results of this investigation, these findings constitute some of the strongest published evidence of dissimilarity in co-

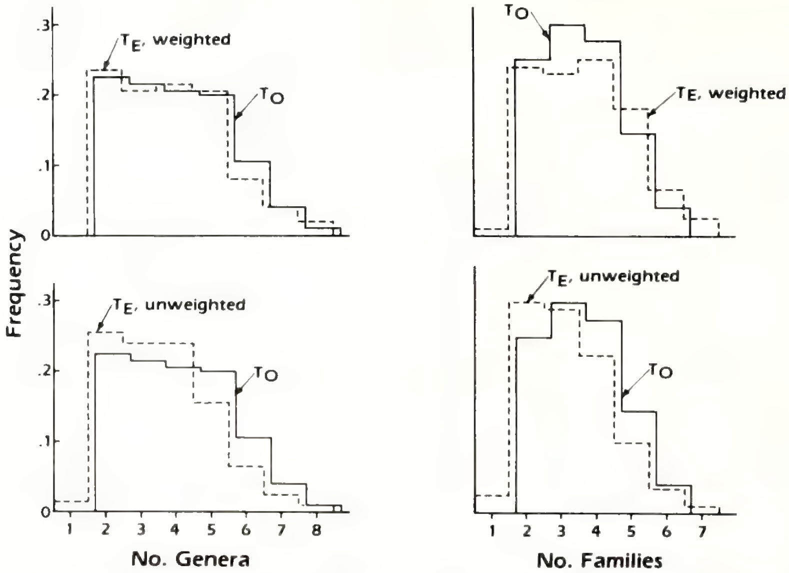

Fig. 1. Comparison of observed (T_O) and expected (T_e) distributions of gastropod samples from Oneida Lake, New York, by the number of higher taxa they contained. The T_e distributions are distinguished by a dashed line and are offset slightly from the T_O distributions.

occurring animals. Most workers (Simberloff, 1970; Strong *et al.*, 1979; Ricklefs and Travis, 1980; Ricklefs *et al.*, 1981; Simberloff and Boecklen, 1981) have found greater than expected similarity in samples of co-occurring animals.

But competition is only one of several possible explanations for the Oneida Lake results. For example, suppose that a pair of congeneric species are found to occupy different habitats, say sandy bottom and rocky bottom, such that they rarely co-occur. It could be that one species competitively excludes the other, or that the two species have adapted to different habitats as a response to competition in the past. Or it could be that the two species have diverged from a single ancestral species that previously occupied both bottom types, and competition has never played a role. Statistical tests such as the one described here are but a preliminary step towards the understanding of a very complex question.

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ENVIRONMENTAL INDUCTION OF SHELL MORPHOMETRIC VARIATION IN THE EUROPEAN STREAM LIMPET, *ANCYLUS FLUVIATILIS* (MÜLLER) (PULMONATA: BASOMMATOPHORA)

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ABSTRACT

Specimens of *Ancylus fluviatilis* were collected in the late spring to early summer of 1979, 1982 and 1984 from 25 different freshwater habitats (6 sites sampled in 1982 were again sampled in 1984) in the Republic of Ireland. The shell aperture length (AL), aperture width (AW) and height (SH) of each individual was measured to the nearest 0.1 mm. Shell fractional $CaCO_3$ and protein contents were determined by dissolution of shell mineral components in 12% nitric acid. *A. fluviatilis* has an annual life cycle, allowing mean annual population growth rate to be estimated by dividing the mean AL of the adult generation by its estimated life-span from the approximate date of hatching (30 May). Analysis of variance indicated that significant differences ($P < 0.05$) occurred between the mean shell $CaCO_3$ content, AL/SH, AW/SH and AL/AW of the various populations. AL/SH, AW/SH and AL/AW were allometrically related to AL and AL/AW and AW/SH, allometrically related to annual population growth rate. Population mean AL/SH was not correlated with growth rate due to a significant reduction in the relative Al of individuals from faster growing populations. Population mean shell $CaCO_3$ content, AL/AW, AL/SH and AW/SH were found to vary significantly both in closely adjacent upstream and downstream collections from the same river and over time (1982-1984) in the same population. As shell growth rate in freshwater pulmonates is highly correlated with primary productivity, the majority of interpopulation variation in the shell shape of *A. fluviatilis* appears to result from environmentally induced phenotypic plasticity. While the $CaCO_3$ fraction of total shell weight was not correlated with growth rate, total shell $CaCO_3$ weight increased with increased growth rate suggesting that individuals from more productive habitats allocated greater amounts of assimilated energy to shell production. Shell $CaCO_3$ content also varied significantly both by locality (upstream versus downstream) and through time (1982-1984) within populations. The high degree of environmentally induced interpopulation variation in the shell morphometrics of *A. fluviatilis* suggests that intraspecific interpopulation variation in mollusc shells cannot be assumed a *priori* to result from genetic differences (i.e., the result of adaptation to microenvironments or genetic drift). This result has important implications to the study of molluscan fossil lineages.

Freshwater molluscs exhibit extensive intraspecific, interpopulation variation in their shell morphometrics, growth, reproduction, physiology, life history traits and population bioenergetics (for reviews of interpopulation variation in freshwater molluscs see Russell-Hunter, 1961a, 1961b, 1964, 1978, 1983; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983). The basis for such variation has long been a topic of study. As early as 1939 Diver warned that the vast majority of interpopulation variations in species' morphology, ecology and physiology assumed to result from genetic differences between populations could, after careful examination, prove to be non-genetic, environmentally induced phenotypic plasticity in response to subtle microenvironmental variation. Diver (1939) referred to such non-genetic variation as "ecological plasticity." More recently similar reservations about the adaptive significance of intraspecific interpopulation variation have been expressed in detail by Stearns (1980). While carefully controlled

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laboratory rearing and field reciprocal transfer experiments have provided strong evidence for the development of genetically different "physiological races" in freshwater molluscs, the vast majority of intraspecifc, interpopulation variation appears to have its origins in non-genetic environmental influences on phenotypic plasticity (Russell-Hunter, 1964, 1978; Aldridge, 1983; Burky, 1983; McMahon, 1983). Recently, it was shown that presumed extensive genetic differences between the life history tactics of temporary and permanent pond populations of the basommatophoran snail, *Stagnicola (Lymnaea) elodes* (Say) were almost entirely the result of habitat differences in productivity and ambient temperature (Brown, 1983, 1985a). Similarly, interpopulation morphological variation in freshwater molluscs appears to be much greater than isozyme variation (Hornbach *et al.,* 1980; Palgulayan and Enriquez, 1983), implying that morphometric variation has a strong non-genetic, environmental component.

Two aspects of interpopulation morphological variation claimed to have a partial genetic basis in freshwater molluscs are those of variation in shell $CaCO_3$ content and in the shell morphometric ratios: aperture length:shell height or length; aperture width:shell height; and aperture length: aperture width (Russell-Hunter *et al.,* 1967, 1981; Nickerson, 1972; Hunter, 1975; Durrant, 1975; Sutcliff and Durrant, 1977). These interpopulation variations in shell mineral content and morphology have been considered to be genetically based because they were not correlated with the availability of environmental calcium or because they could not be explained by allometry of shell morphology in relation to differences in mean population shell length. However, other studies have shown that shell $CaCO_3$ can be correlated with a number of environmental variables other than Ca^{+2} concentration (Hunter and Lull, 1977) and that shell morphometric ratios can vary within populations between years (Durrant, 1980) or in individuals drawn at different sites along a continuous river population (Durrant, 1975). Such results argue strongly that environmental influences are the primary cause of shell morphometric variation in freshwater molluscs.

One uninvestigated source of non-genetic, interpopulation phenotypic variation in molluscan shell morphmetrics is the possible allometry between shell form and mineral content in relation to shell growth rate. In a review of the allometric growth of molluscan shells, Vermeij (1980) suggested that while there was a strong possibility that shell biometric variation could result from an allometry with growth rate, the relationship between these two variables had not been systematically examined for any molluscan species.

Considering the extensive interpopulation variation in growth rate reported for freshwater molluscan species and its direct correlation with environmental productivity and temperature (Russell-Hunter, 1961a, 1961b, 1978; Aldridge, 1983; Burky, 1983; McMahon, 1983; and references therein) an allometric relationship between shell morphometry and growth rate could account for a large proportion of the intraspecific, interpopulation shell variation previously considered to be genetic. This paper presents an analysis of the relationship between interpopulation variation in shell growth rate and interpopulation variation in shell $CaCO_3$ content and shell morphometric ratios for 25 populations of the freshwater stream limpet, *Ancylus fluviatilis* (Müller), from the Republic of Ireland. The data are utilized to test the hypothesis that the vast majority of interpopulation shell variation in this species can be explained by non-genetic, phenotypic plasticity in response to microenvironmental variation that affects mean population shell size and shell growth rate, and does not require explanations based on genetic mechanisms such as founder effects, genetic drift, and/or natural selection.

METHODS

Specimens of *Ancylus fluviatilis* were collected from 25 isolated freshwater drainage systems in the Republic of Ireland (Table 1, Fig. 1). The majority of collections were made during June and July, with the exception of collections 43, 44, and 46 (Table 1) which were made in late fall or early spring. The 1979 collections were taken from eight sites throughout Ireland (sites 43-50, Fig. 1). In 1982 and 1984 the remaining collections were focused on sites in northwest Ireland, particularly in the southern portion of County Donegal (Fig. 1, sites 1-40). The 1982 collections were taken from 9 sites in County Donegal. Six of the sites collected in 1982 were recollected in 1984 (sites 3&23R, 6&26R, 7&27R, 8&28R, 9&29R, and 11&31R, Fig. 1 and Table 1) along with an additional eight previously uncollected sites (sites 32-39, Fig. 1 and Table 1). The 1984 collecting sites included upstream and downstream stations on the Glennaddragh River separated by 2 km (sites 30 and 39) and the Croleavy Lough Outlet separated by 0.8 km (sites 31R and 32) both in Southern Donegal (Fig. 1).

With the exception of the two upstream-downstream sites, all collection sites were on drainage systems completely isolated from each other from head waters to marine outlets. Therefore, endemic populations of the highly aquatic *Ancylus fluviatilis* were reproductively isolated, dispersal between populations occurring only passively on birds or water beetle elytra (Russell-Hunter, 1978).

Snails were collected by lifting rocks and other hard surfaced debris gently from the substratum and removing all attached individuals by sliding a scalpel blade under the anterior shell edge. Specimens were immediately fixed in 12% (by volume) neutralized formaldehyde and later transferred to 70% alcohol. Sample size ranged from 16 individuals at site 45 to 247 individuals at site 39 (Table 1).

The shell aperture length (AL, the greatest anterior-posterior distance across the aperture), aperture width (AW, the greatest distance across the aperture 90° to the anterior-posterior axis) and shell height (SH, the greatest vertical distance from the apex of the shell to the plane of the aperture) (Fig. 2) of each individual were measured to the nearest 0.1 mm at 10X with an eyepiece micrometer in a binocular dissecting microscope. SH was measured by moving an individual from a water filled measuring dish up the side of a vertically mounted glass cover slip with a small brush. Water surface tension allowed moistened specimens to adhere to

Table 1. Site number (R designates a 1982 site collected again in 1984), site location, generations in sample (A = previous year's adults, J = that year's juveniles), number of sampled individuals in a generation (n), mean generation aperture length (AL), and standard deviation (s.d.) of AL in populations of the European stream limpet, *Ancylus fluviatilis*, collected in the Republic of Ireland.

Site	Location	County	Date of Collection	Generations in Sample	n	Mean AL (mm)	s.d.
1	Spring, Slieve League Mountain	Donegal	29/6/1982	1981A	31	2.95	±0.44
2	Unnamed stream I, Derrylahan	Donegal	05/7/1982	1981A	47	4.28	±0.45
				1982J	70	1.37	±0.26
3	Unnamed stream I, Cashel	Donegal	13/7/1982	1981A	27	4.46	±0.87
				1982J	95	1.77	±0.46
4	Unnamed stream II, Cashel	Donegal	13/7/1982	1981A	35	4.35	±0.30
				1982J	37	1.67	±0.49
6	Glen River, Straboy	Donegal	05/7/1982	1981A	57	3.93	±0.52
				1982J	25	1.28	±0.17
7	Gannew Brook, Mennacross	Donegal	05/7/1982	1981A	50	4.49	±0.66
				1982J	15	1.37	±0.20
8	Unnamed stream II, Derrylahan	Donegal	06/07/1982	1981A	44	5.36	±0.56
				1982J	68	1.93	±0.44
9	Unnamed stream, Fintragh, Killybegs	Donegal	08/7/1982	1981A	45	4.48	±0.70
				1982J	26	1.60	±0.47
11	Croleavy Lough Outlet, Teelin	Donegal	08/7/1982	1981A	45	4.08	±0.53
				1982J	37	1.78	±0.47
23R	Unnamed stream, Cashel (site 3)	Donegal	29/6/1984	1983A	52	4.22	±0.84
				1984J	94	1.89	±0.52
26R	Glen River-Upstream, Straboy (site 6)	Donegal	03/7/1984	1983A	59	3.84	±0.43
				1984J	2	1.25	±0.70
27R	Gannew Brook, Mennacross (site 7)	Donegal	03/7/1984	1983A	49	4.63	±0.56
				1984J	21	1.60	±0.22
28R	Unnamed stream II, Derrylahan (site 8)	Donegal	30/6/1984	1983A	16	5.64	±0.56
				1984J	21	1.84	±0.54
29R	Unnamed stream, Fintragh, Killybegs (site 9)	Donegal	02/7/1984	1983A	30	4.18	±0.57
				1984J	50	1.58	±0.41
31R	Croleavy Lough Outlet Upstream, Teelin (site 11)	Donegal	03/7/1984	1983a	55	3.72	±0.58
				1984J	46	1.67	±0.32
32	Croleavy Lough Outlet Downstream, Teelin	Donegal	03/7/1984	1983A	45	4.30	±0.56
				1984J	52	1.58	±0.37
33	Owenwee River, Carrick	Donegal	03/7/1984	1983A	8	3.90	±0.68
				1984J	69	2.08	±0.41
34	Lough Inch, Trusky Road, Galway	Galway	27/6/1984	1983A	35	4.05	±0.69
				1984J	1	1.20	—
35	Unnamed stream I, Doonin	Donegal	29/6/1984	1983A	52	4.95	±0.64
				1984J	97	1.70	±0.41
36	Unnamed stream, Cladigh Na g'Caoire	Donegal	29/6/1984	1983A	54	3.94	±0.53
				1984J	43	1.62	±0.37
37	Unnamed stream III, Derrylahan	Donegal	30/6/1984	1983A	43	5.36	±0.65
				1984J	43	1.56	±0.26
38	Unnamed stream II, Doonin	Donegal	30/6/1984	1983A	61	4.51	±0.66
				1984J	19	1.45	±0.26
39	Glennaddragh River, Upstream, Kilcar	Donegal	02/7/1984	1983A	52	4.53	±0.57
				1984J	195	1.99	±0.57
43	Glencullen River, Eniskerry	Dublin	22/11/1978	1978A	188	4.06	±0.70
44	Owen Doher River, Tibradden	Dublin	09/11/1978	1978A	61	3.60	±0.45
45	Little Brosna River, Riverstown	Tipperary	13/6/1979	1978A	15	6.69	±1.13
				1979J	1	1.20	—
46	Unnamed stream, Sherkin Island	Cork	15/3/1979	1978A	29	2.93	±0.73
47	Woodford River, Woodford	Galway	13/6/1979	1978A	35	5.92	±1.21
				1979J	11	1.25	±0.15
48	River Liffey, Lucan	Dublin	09/6/1979	1978A	27	6.48	±1.39
				1979J	73	1.23	±0.32
49	Aille River, Doolin	Clare	14/6/1979	1978A	64	4.11	±0.71
				1979J	2	1.20	±0.00
50	Nore River, Castletown	Offaly	14/6/1979	1978A	44	4.64	±0.91
				1979J	22	1.70	±0.32

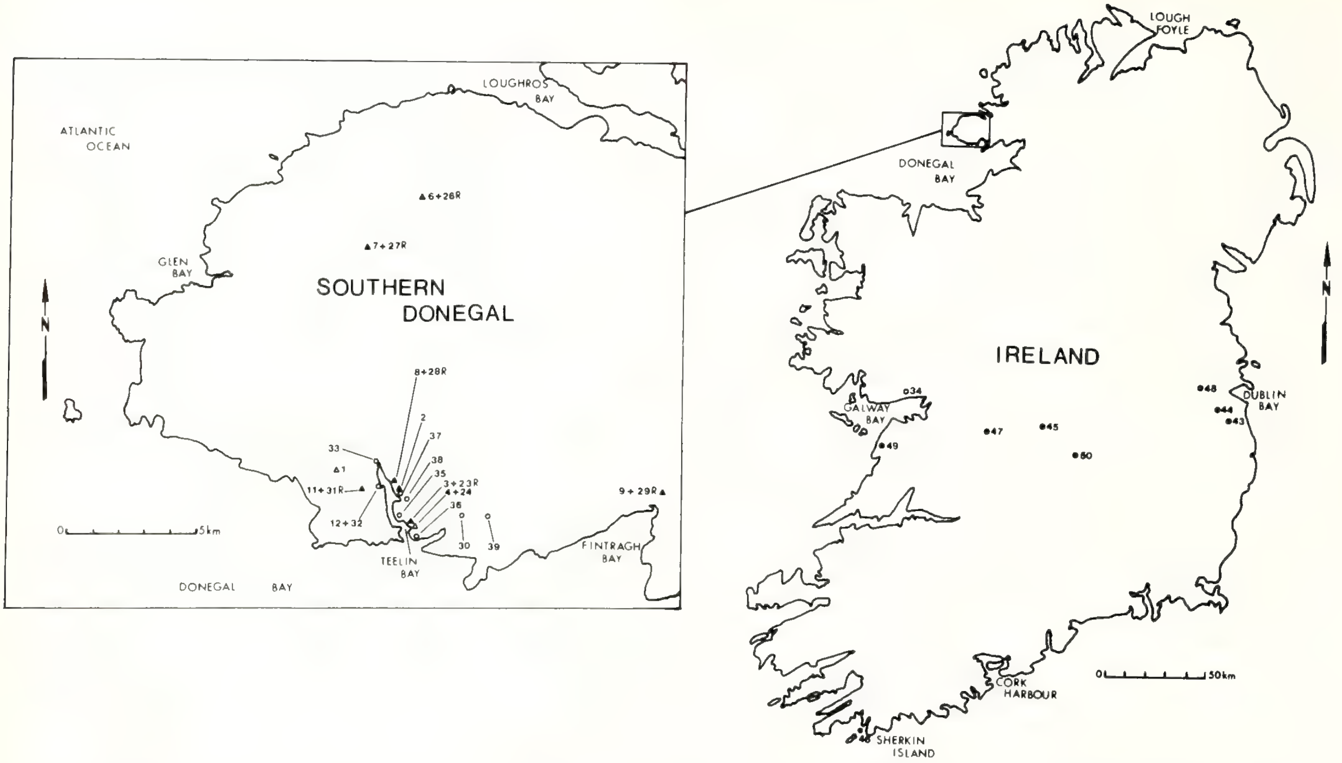
ATLANTIC OCEAN
LOUGHROS BAY
GLEN BAY
SOUTHERN DONEGAL
▲6+28R
▲7+27R
8+28R
2
37
38
35
3+23R
▲+24
36
33
△1
11+31R
12+32
30
39
9+29R▲
TEELIN BAY
FINTRAGH BAY
DONEGAL BAY
0 5km
N
LOUGH FOYLE
DONEGAL BAY
IRELAND
GALWAY BAY
34
49
47
45
50
48
44
43
DUBLIN BAY
CORK HARBOUR
SHERKIN ISLAND
46
0 50km
N

Fig. 1. Map of Ireland showing the locations of collected populations of *Ancylus fluviatilis*. Insert on the left is an expanded portion of the map showing the location of collection sites in southern Co. Donegal. Solid circles indicate populations collected in late 1978 and 1979, open triangles, populations collected in 1982, open circles, populations collected in 1984 and solid triangles populations collected in both 1982 and 1984. Numbers next to collection sites can be used to identify site locations listed in Table 1.

the vertical surface of the cover slip during measurement.

For each sample the number of individuals in each 0.1 millimeter AL size class were expressed as a percentage of the total sample size and plotted as size-frequency polygons in 1 mm intervals (after Russell-Hunter, 1953). Visual examination of these polygons allowed samples to be divided into adult and juvenile size classes. As *Ancylus fluviatilis* is an annual species (Russell-Hunter, 1953; Geldiay, 1956; McMahon, 1980), samples taken in the late spring and early summer were characterized by the presence of two cohorts of individuals marked by distinctly different, non-overlapping distributions of AL. A cohort of larger individuals represented the adults of the previous year's generation and a cohort of smaller individuals represented recently hatched juvenile snails from the oviposition of the previous year's adults (Russell-Hunter, 1953). For Irish populations of *A. fluviatilis* oviposition is initiated in late April to mid-May and hatching occurs approximately two to three weeks later (McMahon, unpublished observations). Similar life cycles have been reported for British populations of this species (Russell-Hunter, 1953; Geldiay, 1956). Therefore, the mean growth rate of the adult generation in each population of *A. fluviatilis* was estimated by dividing the mean AL of that generation by the number of days between an approximate hatching date of 30 May and the subsequent date on which a population was sampled. Multiplying this daily growth rate figure by 30

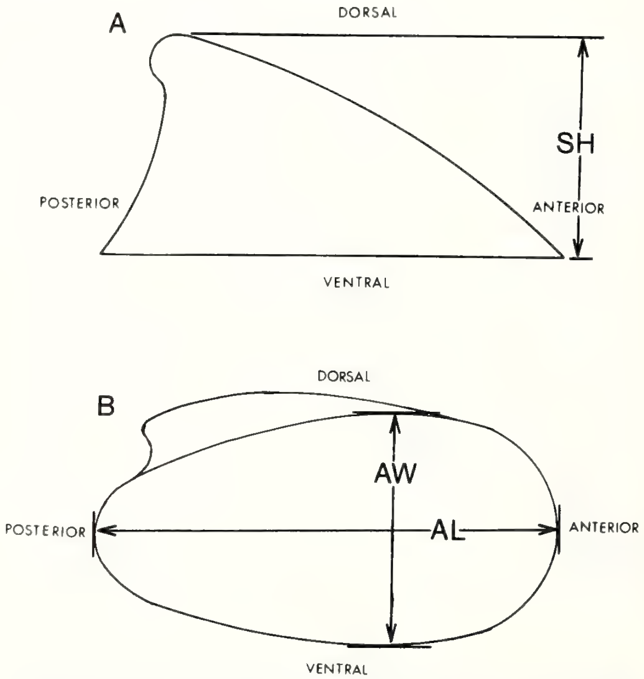
A
DORSAL
SH
POSTERIOR
ANTERIOR
VENTRAL
B
DORSAL
AW
POSTERIOR
AL
ANTERIOR
VENTRAL

Fig. 2. Linear dimensions measured on the shells of *Ancylus fluviatilis*: AL = aperture length; AW = aperture width; and SH = shell height.

Table 2. Shell morphormetric ratios of Irish populations of the European stream limpet, *Ancylus fluviatilis*, in relation to estimated adult growth rate (mm SL/30 days): Gen. = year of collection and generation (i.e., A is adults of the previous year; J is that year's juveniles); mean shell CaCO$_3$ content = mg shell CaCO$_3$/mg total shell dry weight; AL/AW = mm shell aperture length/mm shell aperture width; AL/SH = mm shell aperture length/mm shell height; and AW/SH = mm shell aperture width/mm shell height. Ratios of AL/AW, AL/SH and AW/SH were estimated for a standard individual with an SL of 4.5 mm from appropriate regressions versus SL for each population (s.e. = standard error).

Site No.	Gen.	mm SL/ 30 days	n	Mean Shell CaCO$_3$ Content (s.e.)	n	AL/AW (s.e.)	AL/SH (s.e.)	AW/SH (s.e.)
1	1981A	0.225	—	——— ———	31	1.38 (±0.012)	2.22 (±0.064)	1.61 (±0.044)
2	1981A	0.321	2	0.937 (±0.005)	117	1.27 (±0.007)	2.21 (±0.038)	1.73 (±0.033)
3	1981A	0.328	5	0.966 (±0.004)	122	1.34 (±0.008)	2.10 (±0.051)	1.57 (±0.035)
4	1981A	0.320	4	0.961 (±0.004)	72	1.31 (±0.009)	2.18 (±0.043)	1.66 (±0.035)
6	1981A	0.295	4	0.903 (±0.005)	82	1.32 (±0.010)	2.25 (±0.033)	1.71 (±0.025)
7	1981A	0.337	10	0.957 (±0.003)	65	1.31 (±0.008)	2.11 (±0.023)	1.61 (±0.025)
8	1981A	0.401	4	0.949 (±0.005)	112	1.30 (±0.005)	2.30 (±0.025)	1.77 (±0.025)
9	1981A	0.334	5	0.963 (±0.004)	73	1.32 (±0.010)	2.16 (±0.040)	1.63 (±0.035)
11	1981A	0.302	4	0.969 (±0.002)	115	1.32 (±0.008)	2.16 (±0.048)	1.63 (±0.035)
23R	1983A	0.321	5	0.953 (±0.005)	146	1.34 (±0.008)	2.07 (±0.025)	1.54 (±0.025)
26R	1983A	0.289	4	0.934 (±0.006)	61	1.31 (±0.010)	2.24 (±0.020)	1.71 (±0.018)
27R	1983A	0.349	5	0.957 (±0.005)	70	1.29 (±0.006)	2.21 (±0.015)	1.72 (±0.013)
28R	1983A	0.428	4	0.960 (±0.003)	87	1.30 (0.010)	2.30 (±0.045)	1.78 (±0.031)
29R	1983A	0.316	5	0.962 (±0.005)	80	1.33 (±0.013)	2.22 (±0.030)	1.67 (±0.025)
31R	1983A	0.280	5	0.972 (±0.002)	101	1.31 (±0.010)	2.20 (±0.033)	1.67 (±0.028)
32	1983A	0.324	5	0.981 (±0.003)	97	1.30 (±0.010)	2.25 (±0.050)	1.73 (±0.038)
33	1983A	0.294	1	0.959 ————	77	1.33 (±0.018)	2.26 (±0.050)	1.60 (±0.044)
34	1983A	0.301	5	0.961 (±0.003)	36	1.30 (±0.007)	2.17 (±0.047)	1.66 (±0.042)
35	1983A	0.377	4	0.955 (±0.002)	149	1.29 (±0.005)	2.15 (±0.025)	1.67 (±0.025)
36	1983A	0.300	4	0.948 (±0.004)	97	1.30 (±0.011)	2.09 (±0.033)	1.60 (±0.025)
37	1983A	0.407	5	0.949 (±0.005)	86	1.30 (±0.008)	2.19 (±0.023)	1.69 (±0.013)
38	1983A	0.343	5	0.959 (±0.003)	80	1.27 (±0.005)	2.16 (±0.015)	1.69 (±0.015)
39	1983A	0.342	4	0.934 (±0.006)	247	1.30 (±0.005)	2.14 (±0.025)	1.64 (±0.018)
43	1978A	0.591	4	0.969 (±0.002)	188	1.26 (±0.003)	2.15 (±0.015)	1.71 (±0.010)
44	1978A	0.667	3	0.962 (±0.004)	61	1.27 (±0.010)	2.25 (±0.035)	1.76 (±0.033)
45	1978A	0.531	5	0.956 (±0.003)	16	1.30 (±0.015)	2.21 (±0.031)	1.70 (±0.026)
46	1978A	0.274	1	0.981 ————	29	1.31 (±0.017)	2.21 (±0.044)	1.69 (±0.042)
47	1978A	0.470	5	0.962 (±0.007)	46	1.30 (±0.010)	2.37 (±0.031)	1.83 (±0.025)
48	1978A	0.518	5	0.962 (±0.003)	100	1.28 (±0.008)	2.19 (±0.018)	1.72 (±0.025)
49	1978A	0.325	4	0.959 (±0.004)	66	1.29 (±0.008)	2.03 (±0.025)	1.58 (±0.019)
50	1978A	0.367	5	0.970 (±0.002)	66	1.29 (±0.008)	2.23 (±0.025)	1.73 (±0.025)

provided a relatively accurate estimate (± 8%) of mean annual population growth rate in mm AL/30 days. Shell morphometric ratios of AL/AW, AL/SH and AW/SH were then computed for each individual in a population sample. Subsequently, means of these ratios were computed for adult and juvenile cohorts in each collection.

For all samples except that from site 1, shell mineral and organic content of 1-5 subsamples (depending on the number of large individuals in the sample, AL > 3.0 mm) were analyzed by the method of Hunter and Lull (1976). Subsamples for shell component analyses consisted of individuals whose aperture lengths were within ± 0.3 mm of a chosen AL. Subsamples were selected to represent the range of AL in the adult generation of any one sample. The flesh of each individual in a subsample was gently removed from the shell with a pair of fine forceps. The shells were then given two 15 min rinses in distilled water, and subsequently dried to constant weight at 90°C. Thereafter, the mineral ($CaCO_3$) component of each subsample of shells was dissolved in 12% by volume nitric acid. After shell dissolution the remaining organic periostracum and attached organic shell matrix were rinsed three times in distilled water (30 min each for a total of 90 min). The remaining shell organic material was blotted on filter paper and dried to constant weight at 90°C. The weight of the $CaCO_3$ component was estimated by subtracting the dry weight of the remaining shell organic component from total shell dry weight. The shell $CaCO_3$ content of each subsample was expressed as a fraction of total shell dry weight.

RESULTS

Of the 33 collections of *Ancylus fluviatilis,* all but six contained individuals of both adult and juvenile generations (Table 1). Of these six, two consisted only of juveniles spawned that spring (site numbers 30 and 40, Table 1) and four consisted only of the adult generation collected prior to the hatching of juveniles (site numbers 1, 43, 44, and 46, Table 1). The mean shell length of the adult generation in the collections varied by over two fold, ranging from 2.95 mm (site 1) to 6.69 mm (site 45) (Table 1). When 30 May is assigned as an arbitary date for the appearance of a new cohort of juveniles in these *A. fluviatilis* populations (see methods) the annual estimated shell growth rates of adult generations varied nearly three fold from 0.225 mm AL/30 Days (site 1) to 0.667 mm AL/30 Days (site 44) (Table 2). The mean shell growth rate for the adult generation of all collections with the exception of those repeated in 1984 (collections 23R, 26R, 27R, 28R, 29R, and 31R, Table 2) was 0.372 mm AL/30 Days (s.d. = ±0.106, n = 25). Differences between the growth rates of populations collected in 1982 and 1984 were very slight compared to the differences in growth rates between populations (Table 2), suggesting that intrapopulation variation in growth rate is much less than interpopulation growth rate variation. The mean difference in growth rate between populations collected in Donegal in 1982 and in 1984 was 0.015 mm AL/30 Days (s.d. = ±0.008, n = 6, range = 0.006-0.027) or 3.2% of the observed interpopulation variation in shell growth rate across all samples (Table 2).

Least squares linear regression analysis indicated that shell $CaCO_3$ contents were not significantly related ($P > 0.05$) to aperture length both within populations and across all populations (Table 3). Therefore, mean population shell $CaCO_3$ contents were computed from subsample values (Table 2). The mean shell $CaCO_3$ content of subsamples from adult generations (with the exception of site 1 for which collected individuals were too small for accurate shell $CaCO_3$ determinations) varied between 0.903 of total shell dry weight (TSDW) at site 6 and 0.981 of TSDW at site 32 (Table 2). When population differences in mean shell $CaCO_3$ content were analyzed for statistical difference by one-way analysis of variance and a Student-Newman-Keuls Test (Zar, 1974) 124 of 435 or 28.5% of the possible pair-wise comparisons between population means proved to be statistically different at the $P \leq 0.05$ level.

Interpopulation variation in the mean shell morphometric ratios of AL/AW, AL/SH and AW/SH of adult

Table 3. Parameters of least squares linear regressions relating shell $CaCO_3$ content and shell morphometric ratios [Aperture Length to Aperture Width (AL/AW), Aperture Length to Shell Height (AL/SH) and Aperture Width to Shell Height (AW/SH)] to aperture length in mm in all individuals of *Ancylus fluviatilis* taken from 33 collections in Ireland: a = Y intercept; b = slope of the regression line; n = sample size; r = correlation coefficient; F = F statistic; and P = probability level.

Regression Variables	a	b	n	r	F	P
Fraction Shell $CaCO_3$ vs. Aperture Length (mm)	0.946	0.0022	132	0.124	3.04	0.084
AL/AW Ratio vs. Aperture Length (mm)	1.249	0.0113	3506	0.260	254.35	<0.0001*
AL/SH Ratio vs. Aperture Length (mm)	2.467	-0.062	3506	0.378	587.04	<0.0001*
AW/SH Ratio vs. Aperture Length (mm)	1.976	-0.065	3506	0.456	921.80	<0.0001*

*Indicates a significant regression at $P < 0.0001$.

generations were tested with one-way analysis of variance and a Student-Newman-Keuls Test of differences between means. The results of this analysis indicated that all three ratios showed significant interpopulation variation. The AL/AW ratio which is an index of the roundness of the aperture showed the least interpopulation variation. Of 465 possible pair-wise comparisons between population means of AL/AW, 119 or 25.6% were significantly different at $P \leq 0.05$. Both AL/SH and AW/SH ratios, which are indices of steepness of the patelliform shell, showed greater interpopulation variation than did the AL/AW ratio. Of the 465 possible pair-wise comparisons of population mean AL/SH and AW/SH ratios, 148 or 31.8% and 153 or 33.1%, respectively, were significantly different ($P \leq 0.05$).

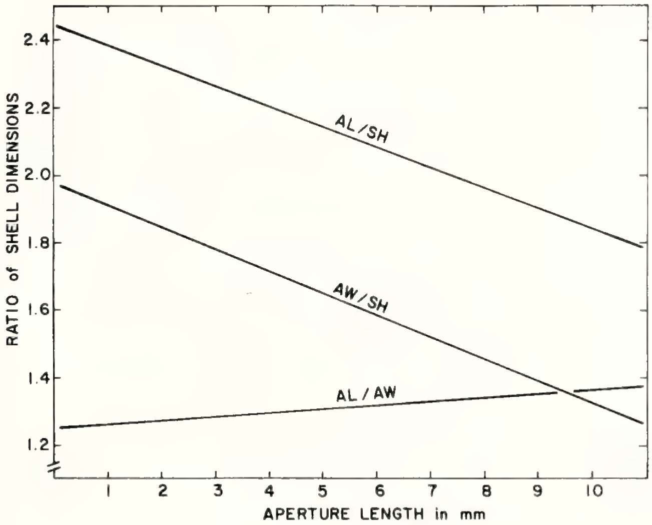

Fig. 3. Allometry of shell morphometric ratios with shell length in all individuals of *Ancylus fluviatilis* collected from 25 populations in Ireland. The y axis is the shell dimension ratios of: aperture length:shell height (AL/SH); aperture width:shell height (AW/SH); and aperture length:aperture width (AL/AW). The solid lines represent best fits of significant ($P < 0.0001$) least squares linear regression equations relating each shell morphometric ratio to shell length in mm (x axis) (see Table 3 for regression parameters.)

Subsequent least squares linear regression analysis indicated that a portion of interpopulation variation in the shell morphometric ratios of *Ancylus fluviatilis* was dependent on shell size, the AL/AW, AL/SH and AW/SH ratios all being significantly correlated ($P \leq 0.05$) with shell size measured as AL within populations. These shell morphometric ratios were also highly correlated with AL ($P \leq 0.0001$) when individual population data were combined across all collections (Table 3, Fig. 3). Regression analysis indicated that the AL/AW ratio increased (the aperture becomes narrower) with increasing AL and that the AL/SH and AW/SH ratios decreased (relative shell elevation increases) with increasing AL (Table 3, Fig. 3). Therefore, the least squares linear regressions relating AL to each of the three morphometric ratios for each individual collection were utilized to predict mean shell morphometric ratios and standard errors for a standard 4.5 mm AL individual from each sample (Table 2). Utilization of a standard sized individual eliminates any bias resulting from differences in adult size distributions of different populations (Table 1) and allows visualization of the allometric relationships not provided by analysis of covariance (Zar, 1974).

Least squares linear regression analysis indicated that the logarithmic transformation of mean population shell $CaCO_3$ content (as % TSDW) was not significantly correlated with the logarithmic transformation of mean population growth rate ($r = 0.135$, $F = 0.519$, $P > 0.5$, $n = 30$) (Table 4). Instead, variation in mean shell $CaCO_3$ content was relatively high between populations with low growth rates (< 0.4 mm AL/30 days) and relatively stable at 96-97% of total shell dry weight in populations with growth rates > 0.4 mm AL/30 Days (Fig. 4).

Least squares linear regressions of shell $CaCO_3$ weight (mg) versus AL for each collection were significant at $P \leq 0.05$. Shell $CaCO_3$ weights of a standard 4.5 mm AL individual estimated from these regressions (with the exception of collections 45 and 48 in which all tested individuals

Table 4. Parameters of least squares linear regressions relating the $\log_{10}$ mean shell $CaCO_3$ content and $\log_{10}$ estimated morphometric ratios of a standard 4.5 mm aperture length individual of *Ancylus fluviatilis* from collections in Ireland to $\log_{10}$ shell growth rate (mm AL/30 Days): AL = aperture length; AW = aperture width; SH = shell height; a = Y axis intercept; b = slope of the regression line; n = sample size; r = correlation coefficient; F = F statistic; and P = probability level.

Regression Variables	a	b	n	r	F	P
Fraction Shell $CaCO_3$ vs. mm AL/30 Days	-0.0149	0.00953	30	0.135	0.519	>0.50
AL/AW Ratio vs. mm AL/30 Days	0.0932	-0.0489	31	0.638	19.881	<0.001*
AL/SH Ratio vs. mm AL/30 Days	0.354	0.0290	31	0.213	1.375	>0.50
AW/SH Ratio vs. mm AL/30 Days	0.264	0.0881	31	0.530	11.329	<0.005*

*Indicates a significant linear regression at $P<0.005$.

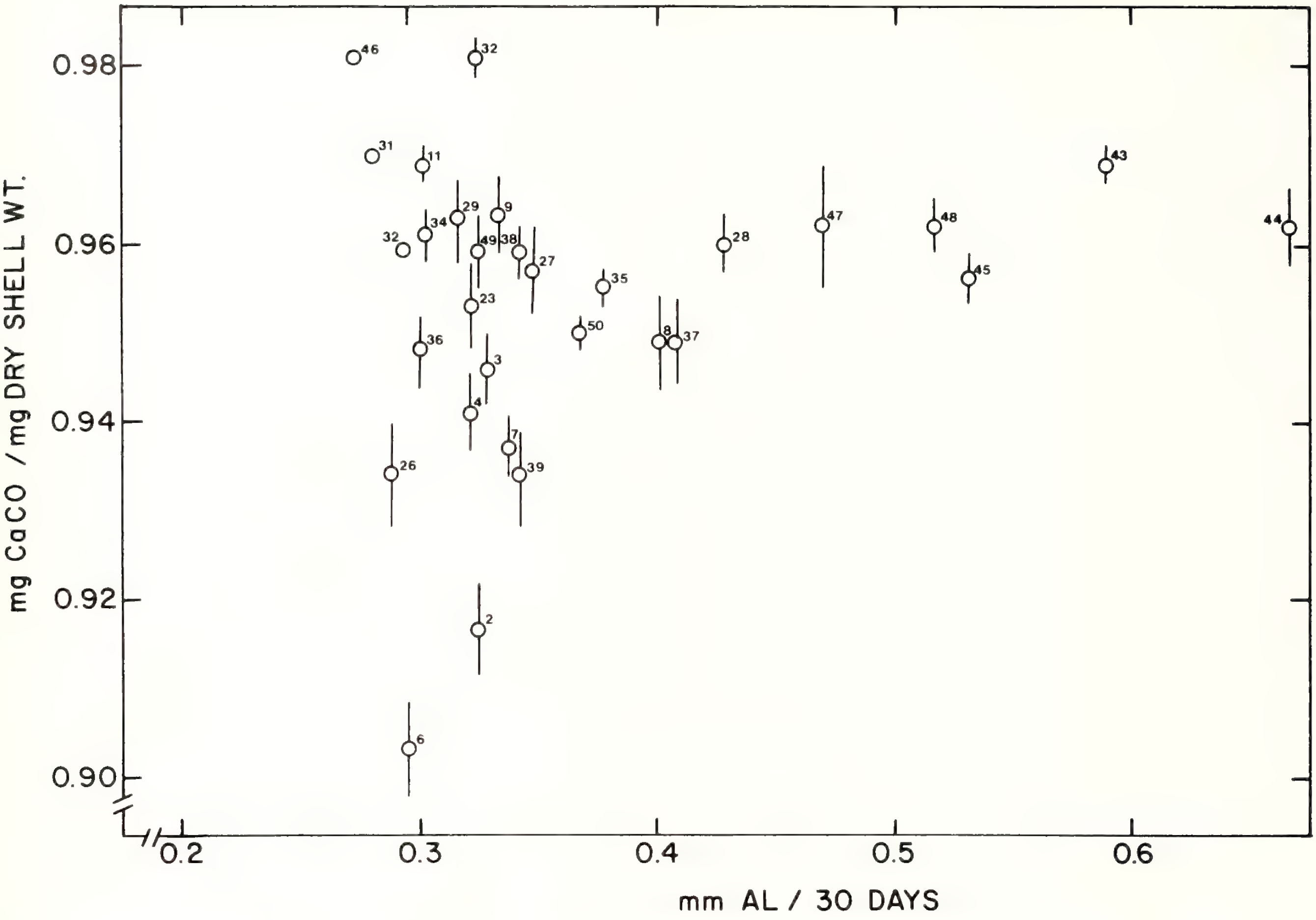

Fig. 4. Interpopulation variation in the population mean shell calcium carbonate content (mg $CaCO_3$/mg total shell weight) (y axis) in relation to annual population shell growth rate in mm aperture length per 30 days (mm AL/30 Days) (x axis) for Irish *Ancylus fluviatilis.* Open circles are mean shell calcium content values of each population for which collection sites are indicated by adjacent numbers (see Tables 1 and 2). Vertical bars are standard errors of the means. No significant correlation ($P > 0.5$) existed between mean population shell calcium carbonate content and growth rate (see Table 4 for regression parameters).

were larger than 4.5 mm Al yielding erroneous estimations of the shell $CaCO_3$ weight of a standard individual) proved to be significantly linearly correlated with annual population growth rate (mm AL/30 days) ($a = 1.55$, $b = 2.98$, $n = 26$, $r = 0.477$, $F = 7.06$, $P < 0.05$) (Fig. 5).

Both the population mean shell AL/AW and AW/SH ratios of a standard 4.5 mm AL individual were significantly ($P < 0.005$) linearly correlated with shell growth rate when ratio and growth rate data were transformed into common logarithms (Table 4). The AL/AW ratio decreased markedly with increasing population shell growth rate ($r = 0.638$, $F = 19.881$, $n = 31$, $P < 0.001$) (Table 4) such that populations characterized by high shell growth rates tended to consist of individuals with rounder shell apertures of greater relative area (Fig. 6). The population mean AW/SH ratio of a standard 4.5 mm AL individual was highly positively correlated with annual population shell growth rate ($r = 0.530$, $F = 11.329$, $n = 31$, $P < 0.005$) (Table 4) such that faster growing populations were characterized by individuals with less elevated patelliform shells (Fig. 7).

Despite the strong linear relationship between the population mean AW/SH ratio and growth rate, the mean population AL/SH ratio was found to be insignificantly linearly related to population mean annual shell growth rate ($r = 0.213$, $F = 1.375$, $n = 31$, $P > 0.5$). Initially this result appeared rather incongruous as the AL/SH ratio, like the AW/SH ratio, is a measure of shell steepness or elevation. It might be presumed that if the AW dimension increases relative to SH in individuals from faster growing populations, then AL should also display a proportionate increase in relation to SH. However, AL decreases relative to AW in individuals from faster growing populations (Fig. 6, Table 4). This decrease in AL relative to AW in individuals from very fast growing populations results in a disproportionate decrease in the AL/SH ratio compared to the AW/SH ratio. Therefore, mean AL/SH ratios of faster growing populations did not increase as population growth rates surpassed 0.5 mm AL/30 days (Fig. 8), resulting in a statistically insignificant relationship between these two variables (Table 4).

Of two different Co. Donegal river populations of *Ancylus fluviatilis* (Glennaddragh River and Croleavy Lough Outlet) collected at upstream and downstream locations, significant variation occurred in the mean shell $CaCO_3$ content of individuals of approximately the same range of SL between adult generations of the upstream (site 31R) and downstream Croleavy Lough Outlet collections (site 32). The mean shell $CaCO_3$ content of individuals from the downstream site (mean $CaCO_3$ content = 0.981) proved significantly greater than that of those from the upstream site (mean $CaCO_3$ content = 0.972) when tested by a Student's t-test ($P < 0.05$) (Zar, 1974) (Table 5).

Significant differences also occurred between the means of all three morphmetric ratios of the 1984 juvenile generations collected at upstream and downstream sites on the Glennaddragh River (Table 5). Comparisons of shell morphometrics of adult individuals could not be made for the Glennaddragh River as adults were not present in the upstream population sample (site 30) (Table 1). Students t-tests indicated that the mean AL/AW ratio was significantly lower and the mean AL/SH , and AW/SH ratios significantly higher ($P < 0.05$) in individuals collected from the upstream site on the Glennaddragh River (site 39) compared to corresponding mean ratios for individuals taken from the downstream site (site 30) (Table 5). As such, individuals from the upstream site had taller shells with narrower apertures than downstream individuals. No significant differences were observed in the shell morphometrics of upstream and downstream collections ($P > 0.5$) in Croleavy Lough Outlet (Table 5).

Student's t-test also revealed significant differences between the mean shell $CaCO_3$ contents and shell morphometric ratios of populations of *Ancylus fluviatilus* collected at the same sites in different years. Of the six populations for which collections were repeated, the mean shell $CaCO_3$ contents of three populations differed significantly ($P < 0.05$) between 1982 and 1984. Mean shell $CaCO_3$ content was greater in adult limpets taken in 1982 (collection 3) than in those taken in 1984 (collection 23R) from the same site in an unnamed stream in Cashel, Co. Donegal, while the mean shell $CaCO_3$ contents of individuals taken in 1982 at both the Glen River, Straboy, Co. Donegal (collection 6) and an unnamed stream in Derrylahan, Co. Donegal (collection 8) were significantly less than those of adults taken at the same sites in 1984 (collections 26R and 28R, respectively) (Table 6). In all cases the differences in mean SL and growth rate of these populations between 1982 and 1984 were negligible (Tables 1 and 2), thus, allometries of shell $CaCO_3$ content or weight could not account for these morphometric differences in shell mineral content.

Of the six recollected populations, a significant dif-

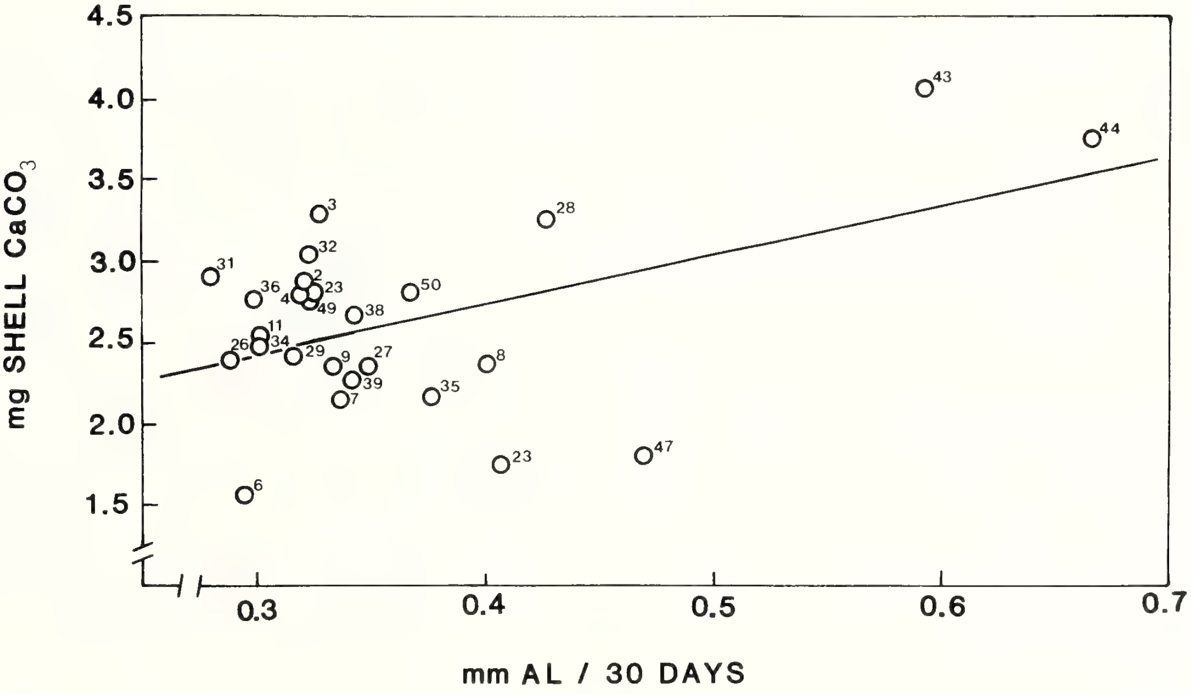

Fig. 5. Allometry of estimated population shell $CaCO_3$ weight (mg) of a standard 4.5 mm AL individual in relation to estimated annual shell growth rate in Irish *Ancylus fluviatilis*. The y axis is mg shell $CaCO_3$ weight estimated for a standard individual from least squares linear regression equations relating mg shell $CaCO_3$ weight to aperture length for each population sampled. The x axis is annual population shell growth rate in mm aperture length per 30 days (mm AL/30 Days). Open circles are the estimated shell $CaCO_3$ weights of a standard 4.5 mm AL individual for each population as indicated by adjacent collection numbers (see Tables 1 and 2). Standard errors about each estimate were smaller than point diameter in all cases. The solid line represents the best fit of a significant least squares linear regression as follows: Shell $CaCO_3$ weight (mg) = 1.55 + 2.98 (mm AL/30 Days) ($r = 0.477$, $n = 26$, $F = 7.06$, $P < 0.001$).

Table 5. Comparison of means of shell $CaCO_3$ content and shell morphometric ratios of aperture length to aperture width (AL/AW), aperture length to shell height (AL/SH) and aperture width to shell height (AW/SH) for Irish populations of *Ancylus fluviatilis* collected at upstream and downstream sites in the same river systems in 1984; n = sample size; s.e. = standard error; and t = t-value.

			Shell $CaCO_3$ Content				Shell Morphometrics									
Site	Site No.	Gen.	$\frac{CaCO_3}{TSW}$	n	s.e.	t-value	n	Mean AL/AW	s.e.	t-value	Mean AL/SH	s.e.	t-value	Mean AW/SH	s.e.	t-value
Glennaddragh River, Upstream	39	1984J	———	—	———	———	195	1.257	±0.005	2.38*	2.316	±0.012	3.91*	1.847	±0.012	4.94*
Glenraddragh River, Downstream	30	1984J	———	—	———	———	129	1.276	±0.016		2.237	±0.016		1.757	±0.014	
Croleavy Lough Outlet, Upstream	31	1983A	0.972	5	±0.002	2.24*	55	1.306	±0.006	0.52	1.726	±0.016	0.52	2.252	±0.020	0.17
Croleavy Lough Outlet, Downstream	32	1983A	0.981	5	±0.003		45	0.301	±0.006		1.736	±0.018		2.257	±0.022	

*Indicates t-values associated with a $P < 0.05$ significant difference between means.

Table 6. Comparison of means of shell $CaCO_3$ content and shell morphometric ratios of aperture length to aperture width (AL/AW), aperture length to shell height (AL/SH) and aperture width to shell height (AW/SL) for Irish populations of *Ancylus fluviatilis* collected in 1982 and recollected in 1984; n = sample size; s.e. = standard error; and t = t value.

		Shell $CaCO_3$ Content				Shell Morphometrics									
Site No.	Date	Mean mg $CaCO_3$/TSW	s.e.	n	t	n	Mean AL/AW	s.e.	t	Mean AL/SH	s.e.	t	Mean AW/SH	s.e.	t
3	13/07/82	0.966	±0.004	5	1.94*	27	1.333	±0.010	0.02	2.062	±0.021	0.28	1.549	±0.020	0.30
23R	29/06/84	0.953	±0.005	5		52	1.333	±0.008		2.053	±0.021		1.541	±0.015	
6	5/07/82	0.903	±0.005	4	3.91**	57	1.316	±0.006	0.46	2.247	±0.014	0.81	1.711	±0.015	0.73
26R	3/07/84	0.934	±0.006	4		59	1.324	±0.017		2.230	±0.016		1.694	±0.018	
7	5/07/82	0.957	±0.003	10	0.04	50	1.328	±0.012	3.08***	2.098	±0.014	15.26***	1.583	±0.013	7.52***
27R	30/06/84	0.957	±0.005	5		49	1.287	±0.005		2.199	±0.013		1.709	±0.011	
8	5/07/82	0.949	±0.005	4	1.83*	44	1.310	±0.009	0.35	2.233	±0.026	0.21	1.709	±0.024	0.08
28R	30/06/84	0.960	±0.003	4		16	1.304	±0.007		2.233	±0.023		1.705	±0.020	
9	8/07/82	0.963	±0.004	5	0.01	45	1.323	±0.007	0.023	2.150	±0.022	1.85*	1.626	±0.017	1.88*
29R	2/07/82	0.962	±0.005	5		30	1.321	±0.009		2.208	±0.021		1.673	±0.016	
11	10/07/82	0.969	±0.002	4	1.08	45	1.317	±0.006	1.37	2.184	±0.015	2.65**	1.660	±0.013	3.16**
31R	3/07/84	0.972	±0.002	5		55	1.306	±0.006		2.252	±0.020		1.726	±0.016	

*Indicates a significant difference between annual collections at $P < 0.05$.

**Indicates a significant difference between annual collections at $P < 0.01$.

***Indicates a significant difference between annual collections at $P < 0.001$.

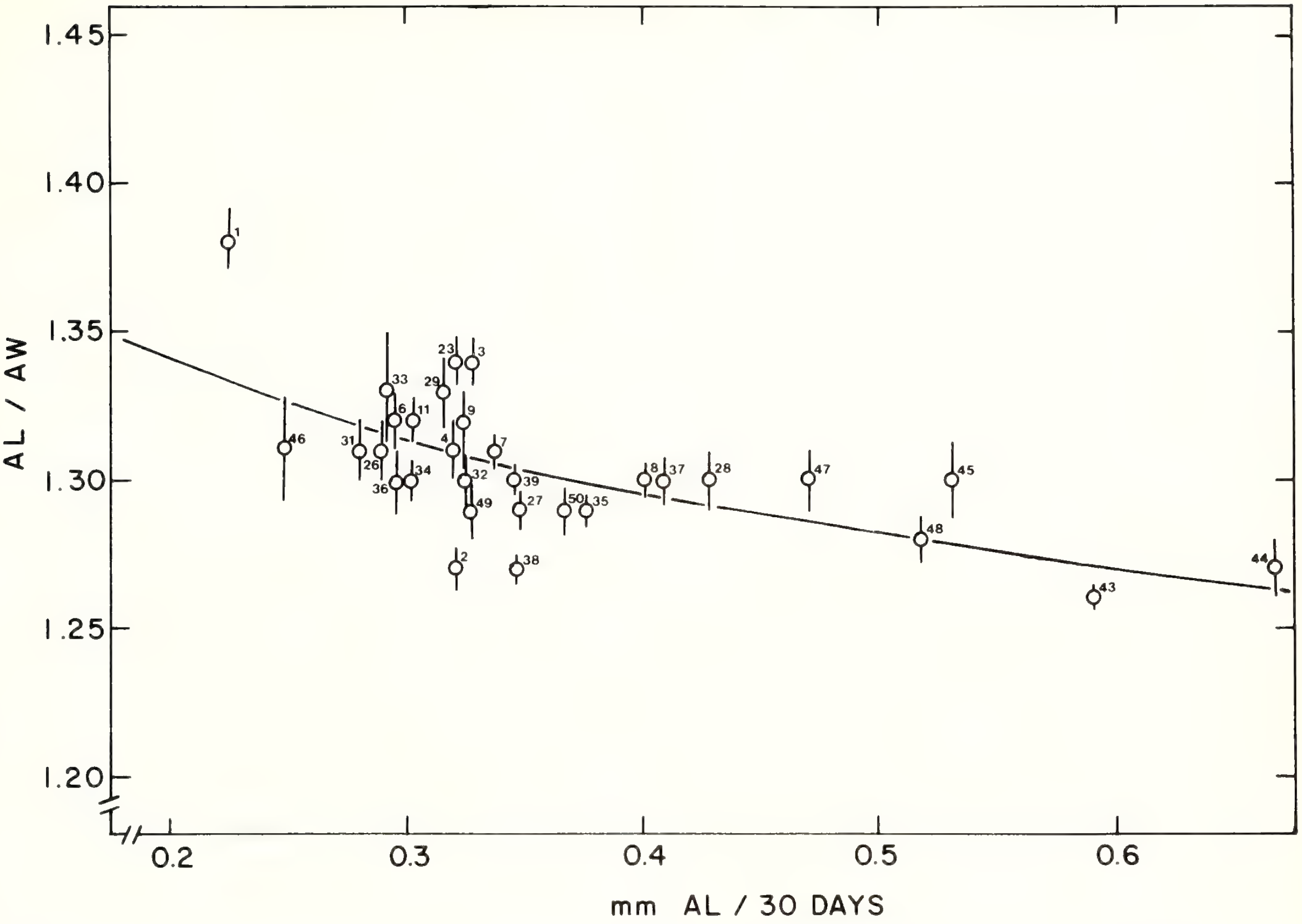

Fig. 6. Allometry of estimated population mean shell length:aperture width ratios (AL/AW) with mean annual population growth rate in Irish *Ancylus fluviatilis* populations. The y axis is the mean shell AL/AW ratio estimated for a 4.5 mm AL standard individual from least squares linear regression equations relating AL/AW to AL for each population collected. The x axis is annual population growth rate in mm AL per 30 days. The open circles are the estimated AL/AW ratio for each population for which collection sites are indicated by the adjacent numbers (see Tables 1 and 2). The vertical bars are standard errors of the means. The solid line represents the best fit of a significant ($P < 0.001$) log-log least squares linear regression equation relating estimated AL/AW to annual population growth rate (see Table 4 for regression parameters).

ference in mean AL/AW ratio of the 1982 and 1984 adult generations was observed only in the Gannew Brook population, Co. Donegal (sites 7 and 27R, Table 6). In this population the mean AL/AW ratio was significantly greater in 1982 (mean AL/AW = 1.328) than in 1984 (mean AL/AW = 1.287) (Table 6). The mean AL/SH and AW/SH ratios of individuals from this population were also significantly greater in 1984 (1982: mean AL/SH = 2.098; AW/SH = 1.583, 1984: mean AL/SH = 2.199, AW/SH = 1.709), indicating that they had less elevated shells with rounder apertures than those taken in 1982 (Table 6). Similar significant increases in the mean AL/SH and AW/SH ratios of adult limpets were also recorded for two other populations in 1984. The mean AL/SH and AW/SH ratios of adult individuals from an unnamed stream in Fintragh, Killybegs, Co. Donegal, were 2.208 and 1.673, respectively, in 1984 (collection 29R), while these values were 2.150 and 1.626 for adults taken in 1982 (collection 9). Similarly, the mean AL/SH and AW/SH ratios of adults taken in 1984 at Croleavy Lough Outlet, Upstream, Co. Donegal (collection 31R) were 2.252 and 1.726, respectively, while those of adults taken there in 1982 (collection 11) were significantly lower at 2.184 and 1.660 (Table 6). None of the significant differences in mean AL/AW, AL/SH and AW/SH ratios observed in populations collected both in 1982 and 1984 could be attributed to allometries associated with changes in mean SL or growth rate between years of collection, as these parameters for the 1981A and 1983A generations at each of these three sites were essentially the same prior to the 1982 and 1984 collections (Tables 1, 2).

DISCUSSION

Russell-Hunter *et al.* (1981) suggest that freshwater molluscs can display four different relationships between shell $CaCO_3$ content and habitat water calcium concentration.

These are: 1. a direct relationship between cell calcium and water Ca^{+2} concentration; 2. regulation of shell $CaCO_3$ content at relatively constant levels over a wide range of environmental Ca^{+2} concentrations; 3. a relation between shell $CaCO_3$ content and trophic conditions (environmental productivity); and 4. great interpopulation variation, but limited intrapopulation variation in shell $CaCO_3$ content reflecting a random geographical distribution of genetic races resulting from founder effects and genetic drift with no obvious adaptive relationship to biotic or abiotic environmental parameters.

Type 1 shell calcium variation is displayed by *Lymnaea peregra* (Müller) (Young, 1975; Russell-Hunter *et al.*, 1981), *Planorbarius corneus* (L.) (Young, 1975), *Biomphalaria pfeifferi* (Krauss) (Harrison *et al.*, 1970), *B. glabrata* (Say) (Thomas *et al.*, 1974), *Cincinnatia cincinnatiensis* (Antony), and a number of sphaeriid and unionid bivalve species (Mackie and Flippance, 1983). Type 2 variation occurs in *Physella gyrina* (Lea) (Hunter and Lull, 1977). Type 3 shell $CaCO_3$ variation occurs in *Helisoma anceps* (Menke) and *Physella integra* (Haldeman) (Hunter and Lull, 1977). Type 4 variation has been reported for *Stagnicola elodes* (Hunter, 1975). A fifth pattern of interpopulation shell variation whereby shell $CaCO_3$ content is inversely proportional to ambient water Ca^{+2} concentration has recently been reported for the sphaeriid bivalves, *Sphaerium simile* (Say), *S. rhomboideum* (Say) (Mackie and Flippance, 1983) and *S. striatinum* (Lamarck) (Burky *et al.*, 1979).

Among ancylid species, the North American stream limpet, *Ferrissia rivularis* (Say), is reported to have a type 4 pattern of interpopulation shell $CaCO_3$ variation. Shell $CaCO_3$ content and organic content (measured in terms of total organic carbon and nitrogen) varied significantly between 10 populations in upstate New York and were neither correlated with each other or with water hardness and dissolved calcium. It was suggested that the synthesis of these two components in this species is under independent genetic controls and that intrapopulation variations in shell $CaCO_3$ and organic contents resulted primarily from differences in the gene pools

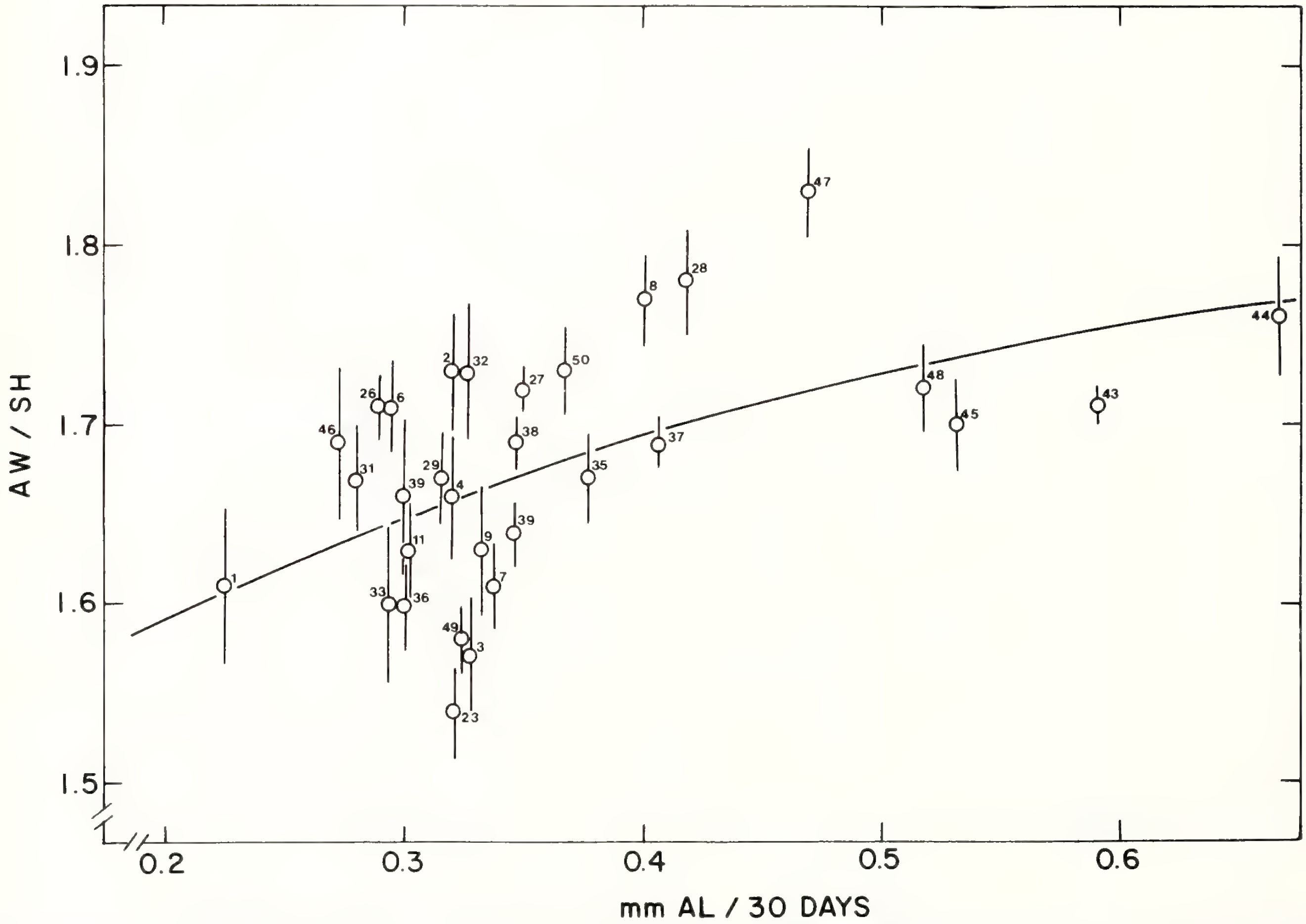

Fig. 7. Allometry of estimated population mean shell aperture width:shell height ratios (AW/SH) with mean annual growth rate in Irish *Ancylus fluviatilis* populations. The y axis is mean shell AW/SH ratio estimated for a 4.5 mm AL standard individual from least squares linear regression equations relating AW/SH to AL for each population collected. The x axis is growth rate in mm AL per 30 days. The open circles are the estimated mean AL/AW ratio for each population for which collection sites are indicated by the adjacent numbers (see Tables 1 and 2). The vertical bars are standard errors of the means. The solid line represents the best fit of a significant ($P < 0.005$) log-log least squares linear regression equation relating estimated AW/SH to annual population growth rate (see Table 4 for regression parameters).

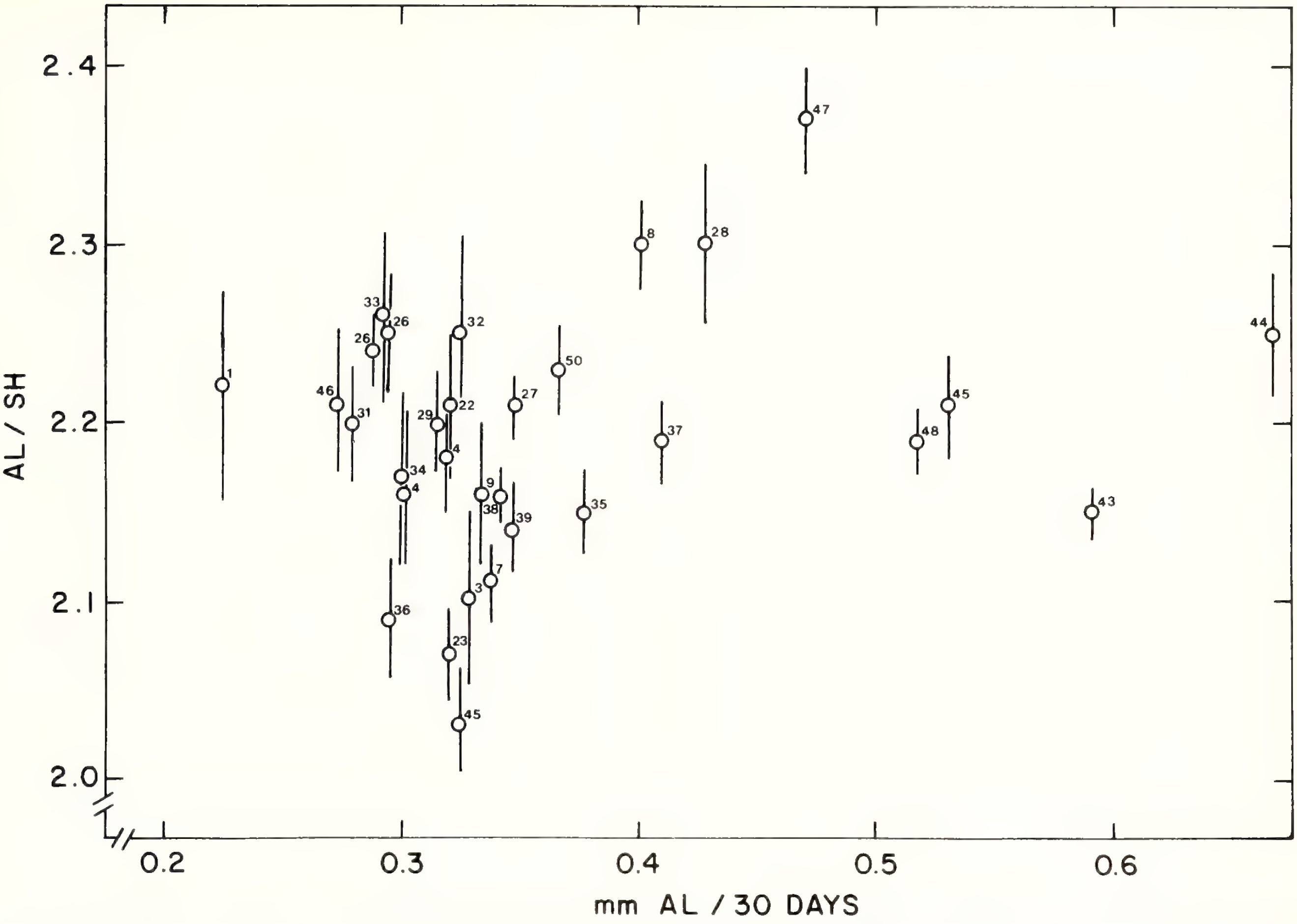

Fig. 8. Interpopulation variation of estimated mean shell aperture length:shell height ratios (AL/SH) in relation to growth rate in Irish *Ancylus fluviatilis*. The y axis is mean shell AL/SH ratio estimated for a 4.5 mm AL standard individual from least squares linear regression equations relating AL/SH to AL for each population collected. The x axis is annual population growth rate in mm AL per 30 days. The open circles are estimated mean AL/SH ratios for each population for which collection sites are indicated by the adjacent numbers (see Tables 1 and 2). Vertical bars are standard errors of the means. There was no significant correlation ($P > 0.05$) between estimated AL/SH ratios and growth rate due to an allometric reduction of AL in relation to AW in faster growing populations (see Results for details and Table 4 for regression parameters).

of reproductively isolated populations (Russell-Hunter *et al.*, 1967, 1981; Nickerson, 1972). In contrast, a direct relationship was found between water Ca^{+2} concentrations and shell $CaCO_3$ content in three populations of the North American pond limpet, *Laevapex fuscus* (C. B. Adams) (McMahon, 1975), indicating that as environmental calcium availability increased so did the amount deposited in the shell. Indeed, such major differences in the patterns of shell $CaCO_3$ content between closely related species occurs more often than not in freshwater molluscs (Burky *et al.*, 1979; Mackie and Flippance, 1983; McMahon, 1983). Differences in the pattern of shell $CaCO_3$ content with ambient Ca^{+2} concentration are even reported between populations of the same species from different geographical areas. Burky *et al.* (1979) report an inverse relationship between shell $CaCO_3$ and environmental Ca^{+2} concentration in populations of *Sphaerium striatinum* from the states of Ohio and New York while Mackie and Flippance (1983) report no correlation between shell $CaCO_3$ and Ca^{+2} concentration for populations of the same species collected in southern Ontario, Canada. Such large variations in the patterns of interpopulation variation of shell $CaCO_3$ content in relation to environmental Ca^{+2} within and between closely related species strongly suggest that abiotic and biotic environmental factors other than Ca^{+2} concentration are acting to induce non-genetic, interpopulation phenotypic plasticity in the shell $CaCO_3$ content of freshwater molluscs.

McMahon (1983) has suggested that interpopulation differences in shell $CaCO_3$ content may be more related to differences in growth rates than to differences in abiotic factors, giving rise to an apparently random (non-adaptive) distribution of interpopulation variation in shell mineral content. In this model faster growing individuals more rapidly expand the mantle edge, and therefore, deposit $CaCO_3$ at the shell edge at a higher rate than slower growing individuals. If deposition of new $CaCO_3$ by the underlying mantle to thicken the shell occurs at relatively the same rate in slow and fast growing individuals, then shells of more slowly growing individuals will be thicker and have proportionately greater $CaCO_3$ contents (an increased fraction of total shell weight will be accounted for by $CaCO_3$). In both *Laevapex fuscus* and *Stagnicola elodes* shell $CaCO_3$ content was inversely correlated with population growth rate (McMahon, 1975; Hunter, 1975). In addition, shell $CaCO_3$ content in both *Physella integra* and *Helisoma anceps* in 7 sympatric populations was shown to be inversely related to habitat primary productivity (Hunter and Lull, 1977). As growth rates in freshwater pulmonates are directly related to environmental productivity (Russell-Hunter, 1964, 1978; McMahon, 1983; McMahon *et al.,* 1974) the decrease in shell $CaCO_3$ content of populations of these two species from more eutrophic waters may be a direct result of increased population growth rates.

Data from this study of *Ancylus fluviatilis* do not support the above hypothesis. No significant correlations could be detected between the fraction of shell $CaCO_3$ and either the estimated population growth rate or size measured as AL. As such, it appears that interpopulation variation in the the shell $CaCO_3$ content in *A. fluviatilis* was not influenced by size, growth rate or, by inference, environmetnal primary productivity. At first, such a result would seem to argue strongly that, as suggested for *Ferrissia rivularis* (Russell-Hunter *et al.,* 1967, 1981; Nickerson, 1972), shell $CaCO_3$ content in *A. fluviatilus* is under relatively rigid genetic control, with observed interpopulation variation the result of gene pool differences between reproductively isolated populations. However, significant differences in shell $CaCO_3$ content were recorded between individuals collected from upstream and downstream sites in 1 of 2 continuous river populations (Table 5) and between individuals taken from the same site in 1982 and 1984 in three of six collected populations (Table 6). Such extensive variations in shell $CaCO_3$ contents at different points in continuous populations and over a time span of only two years the same populations almost certainly resulted from environmental influences operating on phenotypic expression ("ecological plasticity", see Diver, 1939; Stearns, 1980) rather than from genotypic differences due to founder effects, genetic drift or natural selection.

The basis for such environmentally induced variation in shell $CaCO_3$ content remains unclear. However, there is recent evidence that a number of other environmental factors can have greater effect on shell $CaCO_3$ content of freshwater molluscs than either growth rate or ambient Ca^{+2} concentration. Increased current flow has been shown to be correlated with increased shell weight in pisidiid clams (Bailey *et al.,* 1983). Mackie and Flippance (1983) demonstrated that in 11 of 28 species of freshwater molluscs shell $CaCO_3$ mass was correlated with ambient pH, including three gastropod species [*Gyraulus parvus* (Say), *Cincinnatia cincinnatiensis* and *Valvata tricarinata* (Say)]. In only one gastropod species, *C. cincinnatiensis*, was shell $CaCO_3$ mass directly related to water Ca^{+2} concentration while it was related to total hardness in both *G. parvus* and total hardness and alkalinity in *C. cincinnatiensis* (Mackie and Flippance, 1983). Such data indicate that environmental influences on shell calcium content may extend well beyond simple phenotypic correlation with calcium availability.

While the proportion of $CaCO_3$ in the shell of *Ancylus fluviatilis* was not related to population growth rate, the actual weight of $CaCO_3$ in the shell of a standard individual was significantly related to growth rate such that individuals from faster growing populations had shells with a greater mineral weight than those from slower growing populations (Fig. 5). As there was no significant change in the proportions of $CaCO_3$ and protein in the shell with SL or growth rate, increase in shell mineral weight with increased growth rate implies a corresponding increase in shell organic content. The basis for this relationship between shell weight and growth rate in *A. fluviatilis* is unclear. However, if increased growth rates are associated with higher levels of primary productivity that allow relatively greater energy allocation to tissue and shell growth (Russell-Hunter, 1964, 1978; Aldridge, 1983; Burky, 1983; McMahon, 1983; Russell-Hunter and Buckley, 1983), faster growing individuals from energy rich microhabitats could be able to devote proportionately greater levels of energy to the fixation of both shell $CaCO_3$ and organic material, thus, producing thicker, more massive shells than individuals from energy poor habitats. As *A. fluviatilis* is a semelparous annual species, diversion of the majority of non-respired assimilated energy from shell production to tissue growth in food limited, slower growing populations can maximize reproductive effort by maximizing size at oviposition. In contrast, diversion of greater levels of energy to production of a more massive and stronger shell can increase chances of survival to reproduction and, thus, be selected for in more productive, less food limited habitats where individuals can sustain higher growth rates (Stearns, 1980).

A possible source of shell $CaCO_3$ variation which remains uninvestigated in freshwater molluscs is that of calcium content of ingested material. The digestive tract of freshwater pulmonates appears to be highly efficient in uptake of ingested Ca^{+2}, 95% of all ingested Ca^{+2} being absorbed from the gut in *Lymnaea stagnalis* Say (van der Borght and van Puymbroeck, 1966). Indeed, absorption of ingested Ca^{+2} has been shown to account for 20% of shell Ca^{+2} in *L. stagnalis* (van der Borght and van Puymbroeck, 1966). In other basommatophoran species, ingested Ca^{+2} makes up an equal to greater proportion of the shell mineral component dependent on water hardness. In water of low Ca^{+2} concentration ingested Ca^{+2} from a diet of lettuce accounted for 70.4% of shell Ca^{+2} in *L. peregra* and 78.8% in *P. corneus.* Even in a medium of high Ca^{+2} concentration ingested Ca^{+2} accounted for nearly 1/2 the shell Ca^{+2} at 45.6% in *L. peregra* and 46.0% in *Planorbarius corneus* (Young, 1975). As ingested Ca^{+2} can make up the major mineral component of the shell of freshwater gastropods, the Ca^{+2} content of periphyton or detritus on which they feed and even that of the substrata grazed can be more correlated with shell $CaCO_3$ content than ambient water Ca^{+2} concentration, particularly in softer waters where the contribution of ingested Ca^{+2} to the shell is greatest.

Certainly, increased food Ca^{+2} content has long been known to induce the production of heavier shells in land snails

(Oldham, 1929, 1934). As basommatophoran pulmonates evolved from a more terrestrial ancestral stock (McMahon, 1983), shell deposition of ingested Ca^{+2} can remain extremely important in shell formation and, therefore, be a major unaccounted, environmental, non-genetic source of what presently appears to be random genetically controlled interpopulation phenotypic variation in the shell $CaCO_3$ content of freshwater molluscs.

The sources of intraspecific, interpopulation variation in the shell morphometric ratios of freshwater molluscs have received extensive investigation. Early investigators considered shell shape to be rigidly genetically controlled and interpopulation variation the result of natural selection and adaptation to microenvironments (Mosley, 1935). Similar natural selection for shell shape in relation to relative degree of exposure to wave action and crab predation has been considered to account for interpopulation shell morphometric variation in isolated populations of the intertidal prosobranch gastropod, *Nucella lapillus* (L.) (Kitching *et al.*, 1966). However other investigators have indicated that environmental influences could induce a high degree of phenotypic plasticity in shell shape. Boycott (1938) showed that interpopulation differences in spire height disappeared when laboratory stocks of *Lymnaea peregra* from different populations were raised under the same conditions. Interpopulation differences in shell shape associated with degree of wave exposure in *N. lapillus* disappear when snails were reared under similar laboratory conditions (Crothers, 1977). Diver (1939) referred to such environmentally induced, non-genetic, interpopulation variability as "ecological plasticity" and there is extensive literature documenting such plasticity in freshwater molluscs (Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983, and references therein).

One source of non-genetic phenotypic variability in shell morphology lies in allometric change in shell shape as individuals become larger. Thus, in gastropods the ratios of aperture length to shell height (shell height corresponds to shell length in turbinate species), aperture width to shell height, and aperture length to aperture width will linearly vary with shell size (Vermeij, 1980). Such allometric variation in shell morphometric ratios is well documented in freshwater molluscs (Peters, 1938; Nickerson, 1972; Durrant, 1975, 1980; Hunter, 1975). In Irish *Ancylus fluviatilus* the AL/SH and AW/SH ratios declined with increasing aperture length and the AL/AW ratio increased with increasing aperture length both within and across populations (Fig. 3). Thus, larger individuals tended to have steeper shells with narrower apertures. A similar negative allometry of the AL/SH and AW/SH ratios with increasing aperture length has been reported for British *A. fluviatilis.* However, in contrast to our results, the AL/AW ratio was isometric with shell length (Sutcliff and Durrant, 1977). Only the AL/SH ratio declines with increasing AL in the North American stream limpet, *Ferrissia rivularis,* while the ratios of AW/SH and AL/AW are isometric with aperture length (Nickerson, 1972). In *Stagnicola elodes* both the SL/AL and SL/AW ratios increase as individuals grow larger, but the AL/AW ratio remains constant (Hunter, 1975).

As freshwater pulmonates generally display annual life cycles in which adults die soon after spring reproduction (Russell-Hunter, 1961a, 1961b, 1964, 1978), the mean population shell length, and, therefore, the mean shell morphometric ratios of a population can exhibit considerable annual variation. Thus, all interpopulation comparisons of shell morphometric ratios should be based on ratios of standard sized individuals estimated from regressions of linear shell dimensions or morphometric ratios on shell length (Peters, 1938; Nickerson, 1972; Hunter, 1975; Durrant, 1975, 1980; Sutcliff and Durrant, 1977) or on size adjusted means computed from the analysis of covariance of regressions relating shell morphometric parameters for each populations (Zar, 1974).

In both *Ferrissia rivularis* (Nickerson, 1972) and *Stagnicola elodes* (Hunter, 1975) the shape of the aperture (defined by the AL/AW ratio) is reported to be isometric with shell growth. While the level of increase in the AL/AW ratio with shell growth is less than that of the decrease in AL/SH and AW/SH in *Ancylus fluviatilis*, it proved highly significant both within and between samples (Fig. 3, Table 3). Lack of allometric variation in the AL/AW ratio with AL in *F. rivularis* and *S. elodes* led both investigators to conclude that aperture shape was rigidly genetically controlled in these species, and that interpopulation variation in the AL/AW ratio was a result of gene pool differences between populations. In contrast, the shell steepness indices of AL/SH (or SL) and AW/SH (or SL) allometrically varied with the mean shell size of the population and, therefore, variation in these ratios was considered to be a result of non-genetic, environmentally induced plasticity associated with trophic conditions controlling mean population shell size (Nickerson, 1972; Hunter, 1975). Further evidence for the genetic control of aperture shape in these species was provided by reciprocal transfer experiments, whereby newly hatched juvenile snails were transferred between populations and raised in cages along with caged control individuals from the recipient population. Such transfer experiments showed that while the AL/SH and AW/SH ratios, reflecting shell steepness of transferred individuals, approached those of the control recipient populations indicating environmental influence, the aperture shape index (AL/AW) remained similar to that of the source population from which individuals were transferred indicating a relatively rigid genetic control of this morphometric feature (Nickerson, 1972; Hunter, 1975).

Our data do not support a hypothesis of such rigid genetic control of aperture shape in *Ancylus fluviatilis*, instead it appears to be allometric with shell growth rate. Vermeij (1980) has suggested that the allometry of shell morphometrics in molluscs can be highly correlated with growth rate. To date no studies have attempted to correlate the interpopulation variation in the shell morphometrics of freshwater molluscs with interpopulation variation in their growth rates. When the shell shape ratios of AL/SH, AW/SH and AL/AW were estimated for a standard sized individual of *A. fluviatilis* from the appropriate regressions of individual ratios versus AL for each collected population, ratios of AW/SH and AL/AW were found to be significantly correlated with the estimated mean annual shell growth rate (Figs. 6 and

7, Table 4). In addition, lack of significant correlation of the AL/SH ratio to growth rate was found to result from the allometric reduction of relative AL in fast growing populations.

There is extensive evidence that interpopulation variation in growth rates of freshwater gastropods results almost entirely from variations in environmental primary productivity (in terms of food quality and quantity) with faster growing individuals occurring in environments with greater standing crop biomass of periphyton or detritus and/or food sources with higher protein contents (Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983; McMahon *et al.*, 1974; and references therein). For almost all gastropod species tested, reciprocal transferral of individuals from one population to another resulted in transferred individuals growing at rates equivalent to that of the recipient population (Hunter, 1975; Eversole, 1978; Payne, 1979; Aldridge, 1982) including the ancylid limpets, *Ferrissia rivularis* (Burky, 1971; Nickerson, 1972; Romano, 1980) and *Laevapex fuscus* (McMahon, 1975). McMahon *et al.* (1974) demonstrated that the protein content of ingested periphyton was directly correlated with population growth rates in *Stagnicola elodes* and the ancylid limpet, *L. fuscus*. Annual variations in mean population shell growth rates of *Ancylus fluviatilis* and three other freshwater gastropod species were found to be correlated with both average hours of sunshine and average ambient temperature during the growth period (Russell-Hunter, 1953, 1961a), both directly related to primary productivity. Indeed, carefully controlled reciprocal transfer and laboratory rearing experiments have demonstrated that the majority of interpopulation variation in population dynamics, life history tactics and bioenergetics of freshwater gastropods appears to be environmentally induced rather than the result of genotypic differences between populations (Burky, 1971; Nickerson, 1972; Hunter, 1975; McMahon, 1975; Eversole, 1978; Brown, 1979, 1983, 1985a, 1985b; Payne, 1979; Romano, 1980; Aldridge, 1982). As such, the three fold interpopulation variation in estimated annual shell growth rate for Irish populations of *A. fluviatilis* does not appear to reflect genetic differences, but, rather, environmental differences in the primary productivity of their respective environments. Certainly, the highest growth rates were recorded in populations from larger rivers on the eastern coast or in the midlands of Ireland (sites 43, 44, 45, and 48; Fig. 1, Table 2) which were far more productive than small oligotrophic streams and ponds sampled in Counties Galway and Donegal (sites 1-39, Fig. 1, Table 2).

A similar allometry between shell morphology and shell growth rate has been reported for the marine intertidal littorine snail, *Littorina littorea* (L.) in which faster growing individuals from habitats of higher food availability produced shells of relatively greater globosity (i.e., shell width : shell length ratio increased with increased growth rate) (Kemp and Bertness, 1984) which corresponds directly to the increase in the AW/SH ratio observed in faster growing specimens of *Ancylus fluviatilis*. However, faster growing individuals of *L. littorea* also produced relatively lighter shells (Kemp and Bertness, 1984), unlike *A. fluviatilis* in which faster growing populations were characterized by shells with greater relative weights (Fig. 5). Such interspecific differences indicate that growth rate allometries of shell morphometrics in molluscs are probably species specific and like allometries with size (Vermeij, 1980) cannot be generalized for the entire phyletic group.

That interpopulation variation in growth rate exhibited a strong positive correlation with mean population AL/SH ratios and a strong negative correlation with mean population AL/AW ratios indicated that the majority of such variation in *Ancylus fluviatilis* is environmentally induced via the effects of environmental productivity on population growth and mean adult shell length. Therefore, individuals of standard size from fast growing populations tend to have more depressed shells with rounder apertures than those from slower growing populations (Figs. 4, 6).

The influence of environment on shell shape is highly apparent when shell morphometric ratios are compared between individuals taken from upstream and downstream locations in rivers with continuous populations or from the same site in different years. For Irish *Ancylus fluviatilis* the means of all three ratios were found to vary significantly in samples of one of two populations collected at upstream and downstream sites (Table 5), while both mean AL/SH and AW/SH varied significantly between three of six populations sampled in 1982 and 1984 (Table 6). One of six populations sampled in 1982 and 1984 displayed significant variation in the mean AL/AW ratio (Table 6). If any of these three shell morphometric ratios were under rigid genetic control and, therefore, minimally affected by environmental influences, such intrapopulation variation in shell morphometrics would not be expected. It would require the existence of small, discrete, highly genetically isolated populations within single stream or river systems or for individuals and populations to be subject to exceptionally high levels of geographical isolation, natural selection and evolution, respectively. Instead, environmental influences affecting shell shape offer a much more plausible explanation for such variation. Indeed, growth rates have been shown to vary widely in populations of *A. fluviatilis* from the same river system (Maitland, 1965; Durrant, 1975, 1977) and in a single population from year to year depending on annual climatic conditions (Russell-Hunter, 1953, 1961a). Our data indicate that such environmentally induced variation in growth rate would lead to variation in shell morphometrics. However, growth rates varied little in populations of *A. fluviatilis* exhibiting significant shell shape variation across years (Table 2) indicating that environmental influences other than those which alter growth rates can also affect shell morphology.

The apparent allometry of shell shape with growth rate does explain the variation in shell shape reported for *Ancylus fluviatilis* in relation to water flow. Specimens of *A. fluviatilis* from areas of rivers with higher current flow rates are reported to have both steeper shells marked by higher AL/SH and AW/SH ratios with narrower apertures marked by reduced AL/AW ratios compared to those from lower flow areas of the same river (Durrant, 1975). Similarly, specimens of *A. fluviatilis* from impoundments or lentic habitats have flatter shells with rounder apertures than those from lotic habitats (Durrant, 1975, 1977, 1980; Sutcliff and Durrant, 1977). It has been suggested that the steeper shells of lotic individuals are a result of the continuous downward pull of pedal musculature required to maintain attachment in high current flows (Durrant, 1975) or due to differences in the allometric relationship of shell height to aperture width, whereby height increases relative to width at a higher rate in individuals from lotic habitats, as a result of selection for a more streamlined shell, less resistant to the effects of current (Sutcliff and Durrant, 1977). The mean population AL and growth rates of *A. fluviatilis* from more lentic habitats are generally greater than those from lotic habitats (Russell-Hunter, 1953, 1961a, 1961b, 1964; Geldiay, 1956; Maitland, 1965; Durrant, 1975, 1977). This difference in growth rate has been directly attributed to the greater primary productivity of lentic or low flow rate lotic habitats compared to high flow rate lotic habitats (Geldiay, 1956; Russell-Hunter, 1961a, 1961b; Maitland, 1965). The results presented here suggest this sort of shell shape variation between individuals from lentic and lotic habitats is more simply explained by the allometry of shell shape with growth rate whereby faster growing individuals from more productive lentic or low flow habitats characteristically have less steep shells with rounder apertures of greater relative area than do individuals with slower growth rates from less productive high flow lotic habitats (Figs. 6, 7, Table 4).

CONCLUSIONS

While this report has been primarily concerned with the variation in shell morphometrics of *Ancylus fluviatilis,* it also has focused on a major topic in the ecology of freshwater molluscs, the source of their extensive intraspecific interpopulation variation. Such variation exists not only in shell morphology and $CaCO_3$ content, but also in many other aspects of their biology including growth, reproduction, population dynamics, life history traits, physiological responses and bioenergetic budgeting (see Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983; for reviews of intraspecific interpopulation variation in freshwater molluscs). In many such studies variations between populations are assumed to result strictly from genetic differences to which an adaptive significance is assigned *a posteriori* to explain the natural selection pressures leading to such variation. Diver (1939) was among the first to point out that the majority of seemingly genetically controlled interpopulation variation in molluscs may actually be non-genetic phenotypic plasticity (ecological plasticity) in response to subtle environmental variation. Stearns (1980) has recently suggested that developmental and physiological plasticity can explain the majority of interpopulation variation in life history traits. Indeed, environmental, non-genetic influences have been shown to be the major cause of interpopulation differences in shell morphology as rearing under constant laboratory conditions caused phenotypic differences to disappear in the marine species, *Nucella emarginata* (Deshayes) (Palmer, 1985) and *N. lapillus* (Crothers, 1977) and the freshwater pulmonate, *Lymnaea stagnalis* (L.) (Arthur, 1982).

Attempts to assign an adaptive significance to such variation could lead to incorrect and rather anomalous hypotheses regarding the evolution of these traits. This can be particularly true of the utilization of shell morphological variation in the interpretation of molluscan fossil records. If shell growth rate has a significant impact on molluscan shell morphology, as it does in *Ancylus fluviatilis,* any major environmental perturbations effecting shell growth such as changes in annual average temperature, water level, calcium availability and/or primary production could induce profound and immediate changes in a species' shell morphology synchronously over a wide geographic area. The Pleistocene fossil records of 12 species of land snails were characterized by variations in shell size, growth rate, mass and morphology that were clearly associated with climatic change during glacial periods and, therefore, a result of environmentally induced ecophentypic plasticity (Gould, 1970). In the past, such apparently rapid and synchronous changes in the shell morphology of fossil gastropods have been attributed to rapid or "punctuated" allopatric speciation (Eldredge and Gould, 1972; Williamson, 1981). However, if environmental change directly effects shell growth rate, major non-genetic, growth related allometric changes in the shell morphology of molluscan fossil lineages could be misinterpreted as speciation events. Thus, apparent punctuated speciation events marked by relatively rapid change in the shell morphology of a molluscan fossil lineage could, in reality, result from geological or climatic episodes that either inhibit or stimulate shell growth rates (for examples see Gould, 1969a, 1969b, 1971; Eldredge and Gould, 1972) or from changes in food availability associated with changes in lake level (Williamson, 1981). Certainly, growth related ecophenotypic variation could be the source of the punctuated changes in shell morphology reported to occur simultaneously in 13 different molluscan lineages during major lake level transgression-regression episodes in a fossil assemblage from the Turkana Basin (Williamson, 1981), particularly as such major shell morphological changes were associated with "stunting" of shell size (an indication of reduced growth rates) and as new morphotypes appeared in very large populations (Williamson, 1981) resistant to rapid allopatric speciation (Eldredge and Gould, 1972; Gould and Eldredge, 1977). In this assemblage even the parthenogenic species, *Melanoides tuberculata* (Müller), which should not respond rapidly to selective pressures, displayed major variations in shell morphology. In addition, all lineages returned abruptly to ancestral morphology during periods of relative environmental stability (Williamson, 1981). In light of the data presented for *A. fluviatilis*, it is possible that such rapid and simultaneous changes in shell morphology could be explained by non-genetic, allometric mechanisms associated with major changes in population growth rates induced by episodes of environmental stress and/or instability.

Our own research has shown that the majority of interpopulation variation in the shell calcium content and shell shape of *Ancylus fluviatilis* appears to be a result of such phenotypic plasticity, eliminating the necessity of invoking genetically based explanations involving founder effects, genetic drift and/or natural selection. The basis of such interpopulation variation can only be rigorously approached by the development of hypotheses which either carefully consider the possible environmental and allometric causes for such variation, through the utilization of reciprocal transfer of individuals between populations, or by the rearing of individuals from different populations in the laboratory through several generations (McMahon and Burky, 1985). While such carefully controlled *a priori* approaches have revealed hard evidence for isolated cases of genetically based physiological race formation in freshwater molluscs (Forbes and Crampton, 1942; McMahon, 1975, 1976; McMahon and Payne, 1980; Russell-Hunter *et al.,* 1981), the vast majority of such studies, too numerous to cite here (see Russell-Hunter, 1964, 1978; Russell-Hunter and Buckley, 1983; Aldridge, 1983; Burky, 1983; McMahon, 1983, for reviews of the sources of interpopulation variation in freshwater molluscs) have indicated that almost all observed interpopulation variation is the result of environmentally induced phenotypic plasticity. In this regard, Brown (1983, 1985a) in careful reciprocal transfer experiments has demonstrated that the vast majority of interpopulation variation in the life history traits of populations of *Stagnicola elodes,* previously assumed to be the result of natural selection and genotype differentiation, instead resulted from environmental differences in productivity and ambient temperature. Interpopulation variation in the shell morphometrics of *Sphaerium striatinum* has been shown to be much more extensive than isozyme variation (Hornbach *et al.,* (1980) or whole body protein variation in the freshwater pulmonate, *Radix quadrasi* (Bequaert and Clench) (Pagulayan and Enriquez, 1983). Such results imply that the majority of interpopulation shell morphological variation in these species is accounted for by non-genetic environmental factors. Even the frequency distributions of isozymes of lactate dehydrogenase are reported to display extensive annual, environmentally induced variation in *Cepaea nemoralis* (L.) (Gill, 1978). Certainly, the extensive capacity of freshwater molluscs for variation in response to environmental perturbation ultimately has a genetic basis and is subject to natural selection. For many species of freshwater molluscs which inhabit temporally unstable, highly variable habitats (Russell-Hunter, 1964, 1978, 1983; McMahon, 1983) the evolved ability of individuals to compensate or adjust major aspects of their morphology, growth, reproduction, life history traits and physiological responses to a wide range of both short and long term environmental variations is highly adaptive. Such phenotypic plasticity allows species such as basommatophoran snails to successfully invade and inhabit marginal, highly variable, temporally unstable shallow freshwater habitats (Russell-Hunter, 1961a, 1961b, 1964, 1978, 1983; Nickerson, 1972; Brown, 1983, 1985a, 1985b; McMahon, 1983).

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INFECTION AND SUCCESSFUL REINFECTION OF BROWN TROUT [*SALMO TRUTTA* (L.)] WITH GLOCHIDIA OF *MARGARITIFERA MARGARITIFERA* (L.)

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ABSTRACT

Brown trout [*Salmo trutta* (L.)] were successfully reinfected with glochidia of *Margaritifera margaritifera* (L.) in the season following an initial infection. Fingerling trout were exposed to glochidia in September 1982 and, although there was great variation in the numbers on each fish, there was no definite evidence of subsequent decline in glochidial numbers. The glochidia metamorphosed and in May 1983 left the fish, which were retained and reinfected in September 1983. The initial number of glochidia attaching in 1983 was higher than in 1982 but the number present declined to a level similar to that observed the first year. Previous studies have noted that *M. margaritifera* glochidia infect mainly small fish and have suggested that reinfection may be deterred by an immune response, however, our study suggests that, at least in the laboratory, older fish can be successfully reinfected with glochidia.

The freshwater pearl mussel, *Margaritifera margaritifera* (L.), has a holarctic distribution. It lives characteristically in fast running streams but with a glochidial larval stage as an obligate parasite on the gills of salmonid fish (Hendelberg, 1961). In Scotland glochidia are released in a limited period between late July and early September (depending on location) and, if inhaled by a suitable host, attach immediately to the gills. This process is highly inefficient. Once attached to their host, glochidia become encysted, grow slowly until the following May, then drop off as fully metamorphosed free living mussels (Young and Williams, 1984a).

Young and Williams (1984a), studying a largely undisturbed mussel population in northwest Scotland, observed a considerable loss of encysted glochidia from wild brown trout, *Salmo trutta* (L.), between December 1979 and May 1980 and between September 1980 and May 1981, such that only about 5% of the glochidia survived. A similar loss was also noted under laboratory conditions for both brown trout and salmon, *Salmo salar* (L.) (Young and Williams, 1984b). In these cases most fish shed all their glochidia, with those remaining being concentrated on a minority of the hosts, although even these lost some. A similar situation has been observed by other workers (Fustish and Millemann, 1978; Bauer, pers. comm.).

In the wild most small, young fish were infected, whereas most large old fish were not (Young and Williams, 1984a), and other workers, such as Awakura (1968), who studied *Margaritifera laevis* (Haas), have also observed the greater incidence of infection of small fish, but usually under laboratory conditions. Several explanations for this and for the loss of encysted glochidia from their hosts are possible. Only small fish can be near the mussels at the time of glochidial release, or their behaviour patterns can predispose them to infection. Alternatively, larger fish can be less susceptible because of some factor which changes with age (such as epidermal thickness), or possibly because of an immune response which develops after infections in previous years.

In this study brown trout were infected with glochidia in the first year and then retained for reinfection the succeeding year. Progress of each year's infections was monitored.

MATERIALS AND METHODS

Juvenile brown trout with a mean length of 8.7 cm were obtained in September 1982 from a commercial stock, provided by Cantray Fish Farm, Croy, Nairn, Scotland, and were free from obvious signs of disease. Water for the fish farm is obtained from the River Nairn, which is believed not to harbour freshwater mussels; nevertheless, 12 fish were examined and found to be free of glochidia. Throughout the experimental period the fish were kept outside in University aquaria at ambient temperature, were fed a full commercial diet, and had a generous throughflow of water derived from the River Dee. The water was passed through a slow sand filter before supply to remove any possible glochidia. Some fish were kept as uninfected controls under identical conditions.

The fish had grown to an average of 20.0 cm by September 1983, at the time of the second infection. Abnormally large or small fish were discarded.

Several large mussels were obtained from the River Dee in August 1982, kept in aerated river water at ambient temperature and observed daily. When the first glochidia were found in the water, they were examined to confirm that they were unencysted and active. The mussels were then moved into new water and the aeration was stopped, resulting in the mass release of glochidia. These were collected and kept in gently aerated water until used for infections. The same procedure was followed in 1983, except that the mussels came from the nearby River Spey.

In both years pairs of brown trout were infected in buckets of aerated river water which contained approximately 500,000 glochidia/5 *l*. Each fish was exposed to glochidia for 3 minutes before being transferred to a large holding tank. Subsamples of the infective glochidia were taken regularly and glochidia were added, as necessary, to maintain the initial density. Approximately 250 fish were infected in 1982 and 100 in 1983. (This infection was carried out by M.R. Young under British Home Office licence No. SHR 1191).

On the day following infection, and at various intervals thereafter samples of 10 fish in 1982/83 and 5 fish in 1983/84 were selected randomly and killed. Fish were weighed, measured and their gills excised and examined immediately. The small sample sizes were necessary so that sufficient fish remained throughout the projected 2-year experimental period. All attached glochidia were counted and between 30 and 50 removed from the cysts and measured, before they and the gills were fixed in aqueous Bouin's fluid. Note was made of any abnormal or dead glochidia.

All trout surviving the September 1982-May 1983 infection were used for reinfection in September 1983. A small number of these may have lost all glochidia in the course of the first infection (by analogy to fish sampled then), but all received an initial load. Only 18 fish (out of 250) died during the first infection period.

On 15 October 1983 many of the fish were found to have a fungal infection. Moribund fish were removed and the remainder were treated with a 2 mg/*l* malachite green solution for 1 hour. This treatment was repeated twice the following week. Subsequent inspection, including the sample taken on 25 November 1983, revealed no apparent sign that encysted glochidia had been affected by this treatment, in that all appeared live and had grown.

On 28 November 1983 chlorine residues contaminated the water supply and killed all fish being held in the University aquaria, including the infected fish, so terminating the experiment.

RESULTS

Glochidia attached successfully to the gills of the brown trout in both years and the initial numbers of glochidia on the fish are indicated by the day 1 samples (Table 1). As can be seen, significantly more glochidia became encysted in 1983 (range 8789-17751) than 1982 (range 637-2737) (Mann Whitney U-test: $p < 0.001$); however, in both years

Table 1. Glochidia present on brown trout during the two infection periods.

	September 1982-June 1983							September 1983-November 1983		
	Days post infection							Days post infection		
	1	23	50	134	150	190	237	1	20	65
No. of glochidia on each trout	637	59	180	0	1	64		8789	0	0
	868	99	280	0	7	326		10290	0	0
	1060	186	424	0	16	685		14831	0	2915
	1292	204	529	1	28	1354		15475	1823	3325
	1331	271	1435	19	30	1417		17751	3673	3601
	1648	372	1436	25	285	1605	920			
	1846	403	1478	366	302	1779				
	2388	1443	1505	575	497	1934				
	2659	1482	1700	1823	1369	2046				
	2737	1497	2709	2022	2219	2122				
Mean (& median) no. of glochidia/fish	1646.6 (1687.0)	601.6 (778.0)	1167.6 (1444.5)	483.1 (1011.0)	475.4 (1110.0)	1333.2 (1093.0)	— —	13427.2	1099.2	1968.2
Mean (& median) no. of glochidia/infected fish	1646.6 (1687.0)	601.6 (778.0)	1167.6 (1444.5)	690.1 (1011.5)	475.4 (1110.0)	1333.2 (1093.0)	—	13427.2	2748.0	3280.3
Mean longest axis of glochidia - mm	0.07	0.13	0.19	0.20	0.26	0.29	0.35	0.07	0.10	0.18
Mean fish length - cm	8.7							20.0		

the infestation rates were highly variable. The mean number of glochidia per fish fluctuated widely for each subsequent sampling date in the first year's infection, and there was no consistent trend in numbers. In contrast, after infection of fish in September 1983, there was an apparent sharp decline by day 20, and this was substantiated by the sample at day 65. The low sample numbers and high variance of results preclude statistical testing, but the magnitude of the change is readily apparent. In both years, later samples contained some fish with no glochidia, whereas others were heavily infected.

Glochidia resulting from the infection in September 1982 grew quickly before winter, reaching 0.19 mm (mean longest axis) by day 50. Growth resumed in early spring and metamorphosis to free-living mussels occurred in late May 1983. Glochidia which attached in September 1983 grew to 0.18 mm (mean longest axis) by day 65, similar to the growth rate recorded in 1982 and they appeared clear and "healthy", in spite of the treatment for a fungal infection earlier in their development.

No fish died at the time of either infection and all subsequently grew at a rate similar to the uninfected control fish.

DISCUSSION

There are strong similarities between these results and those of other workers. The marked decline in attached glochidia after the initial infestation in September 1983 is similar to that recorded by Fustish and Millemann (1978) [on chinook salmon *Oncorhyncus tshawytscha* (Walbaum) and coho salmon *O. kisutch* (Walbaum)] and Young and Williams (1984a, b). However R. Dettmer (pers. comm.) did not find this with a German population of *Margaritifera margaritifera* on brown trout, where there was no decline from initial levels of 100-200 glochidia on 10 cm fish.

In other studies different species and sizes of host fish have been used, as well as other species of *Margaritifera*. However, the eventual numbers of glochidia per infected fish recorded here are close to the ranges previously reported. Karna and Millemann (1978) reported *Margaritifera* glochidial infections of less than 100 to more than 1000 on 4-7 cm chinook salmon and Fustish and Millemann (1978), working with fish of 4-6 cm, noticed declines from initial mean glochidial loads of 1547 on coho salmon, and 938 on chinook salmon. Young and Williams (1984a) reported wild brown trout with mean natural infections of 923 glochidia per fish in 1979 and 458 per fish in 1980; in both cases a significant reduction followed. The levels of 2750-3300 per 20 cm fish in September 1983 are higher than previously reported, but the fish, at 20 cm, were larger and no fish died at the time of infection. In contrast, Murphy (1942) reported the deaths of 7 cm brown trout infected with 100-295 glochidia of Californian *Margaritifera*, and Meyers and Millemann (1977) also reported fish mortality in various species of experimentally infected fish, some of which proved unsuitable as hosts. The much greater initial loads of glochidia in September 1983 than September 1982 could have been due to a larger available gill area on the larger fish, to a greater volume of water respired by the larger fish, or to increased stress sufferd by larger fish in the buckets (due to lowered oxygen levels and more contact with the other fish), resulting in a higher gill ventilation rate.

Unfortunately it was necessary to use glochidia from mussels from different rivers in 1982 and 1983, although the rivers are in proximity. Different "strains" of *Margaritifera margaritifera* can occur in these two rivers, but Purser (1985) did not detect differences between them using electrophoresis. However Kat (1983) did find differences between nearby *Elliptio* populations in the United States and it is possible that the slightly different infection patterns in 1982 and 1983 reported here were due to differences between the glochidia.

Previous studies have noted that young host fish were both more heavily infected than older fish and that a higher proportion of them were infected (Awakura, 1968; Karna and Millemann, 1978; and Young and Williams, 1984a) and this has been tentatively ascribed to three possible factors. Glochidial release in late summer can occur when only the younger host fish are near the mussel beds. This is feasible in Scotland where adult brown trout tend to live mainly in lochs, returning to streams in winter to spawn after the period of glochidial release (Young and Williams, 1984a). Alternatively, older fish can be inherently less suitable hosts than younger fish due to a thicker mucus layer, epithelium, or other physical feature. Lastly, observations showing hyperplasia and other histological effects associated with glochidiosis suggest that an immune response can be involved (Meyers, *et al.*, 1980). Our results clearly show successful reinfection of 20 cm fish and so suggest that if an immune response is induced by glochidia, then it is weak or transitory. Furthermore there is no physical reason which prevents infection of older fish.

ACKNOWLEDGMENTS

We acknowledge gratefully the technical and secretarial help received here, the permission from various riparian owners to collect mussels, the useful discussions that we had with Drs. L. Laird, C. Secombes, G. Bauer and R. Dettmer, and the helpful comments of referees on early drafts of the paper.

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THE AMERICAN MALACOLOGICAL UNION
52nd ANNUAL MEETING

MONTEREY, CALIFORNIA, U.S.A.
1 - 6 August 1986 July !

Annual Business Meeting Report 131
Financial Report 133
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Full manuscripts of the Opisthobranch Symposium (Organized by Terry Gosliner and Michael Ghiselin) will appear in Volume 5(2) of the *American Malacological Bulletin.*

ANNUAL BUSINESS MEETING
REPORT FOR 1986

The 52nd annual meeting of the American Malacological Union convened at 4 p.m. Saturday, July 5, 1986, in the Monterey Conference Center, Monterey, California, with Dr. James Nybakken presiding. He announced a registration of 178.

Janet R. Voight of the University of Arizona was awarded the $500.00 award for the best student paper presented at this meeting.

Minutes of the 1985 meeting as printed in Vol. 4 (1) of the *Bulletin* were approved.

Recording Secretary Constance E. Boone announced the membership for fiscal year 1985 as 664. Subscriptions totalled 81.

Corresponding Secretary Paula Mikkelsen reported that an update of the book list and dealers' list routinely sent to correspondents had been printed. Sales of *How to Study and Collect Shells* for 1985 totalled $235.25, and sales of Special Edition 1 totalled $1742.81. Two Newsletters cost $1129.35. Correspondence included mailing flyers on the special editions being published by AMU, as well as answering 127 letters of inquiry. This officer maintains the membership mailing lists on Prime 750 computer. There is no cost for maintenance except cost of labels.

Treasurer Anne Joffe announced $21,410.59 in the Symposium Endowment Fund. Her full report on 1985 is printed below.

Editor Robert Prezant announced publication of the *Corbicula* Special Edition, available at this meeting at a discount to members. The Special Edition on Entrainment of Oysters was scheduled for later in 1986. The new printer, Shaughnessy, has provided a much smaller cost for printing the *Bulletin*. All three special editions are being printed with monies provided by funds from the interested organizations, resulting in accumulation of extra funds for the *Bulletin* account. Council has given approval to the addition of an assistant in publishing activities. Dr. Ronald B. Toll of the University of the South, Sewanee, Tenn., will assist the Editor.

Elected for 1986-1987 were the following officers:

President:	William G. Lyons
President-Elect:	Richard E. Petit
Vice-President:	James H. McLean
Corresponding Secretary:	Paula Mikkelsen
Councillors-At-Large:	Carole S. Hickman
	Edward Nieburger
Past President (4-10 years)	Alan Kohn
	Clyde F. E. Roper
Past President (11 years +)	Ruth D. Turner
	Harold D. Murray

Other officers in term and past presidents to serve on Council according to the new structure of Council are listed elsewhere in this issue.

Richard E. Petit's report for the Finance Committee included efforts to increase and maintain membership by issuing invitations to members of related organizations and urging reinstatement.

The Reprint Committee, headed by Petit, announced the printing of "Museum Boltenianum" offered at this meeting. A reprint of Lightfoot's "Portland Catalogue" is in preparation.

Auditing Committee Chairman William G. Lyons announced that the books had been reviewed and were in good order. He noted that a CPA had been used to prepare the report for 1985.

The budget adopted for 1987 follows:

INCOME	
Memberships (all except Life)	$13,000.00
Sales	
HTSCS	250.00
Bulletin Back Issues	1,800.00
Bulletin Supplements	4,000.00
Teskey Index	25.00
SUBTOTAL SALES:	$(6,075.00)
Bulletin Receipts (Page charges, etc.)	$2,500.00
Proceeds of Meeting	3,500.00
Donations, Symposium of that year	1,500.00
Miscellaneous	250.00
Interest, Symposium Endowment Fund	2,000.00
TOTAL:	$28,825.00
Interest—General Savings (Not added to income; includes that from Life Membership Fund)	$2,200.00
DISBURSEMENTS	
Bulletin	$18,000.00
Newsletter	1,500.00
Membership Committee	100.00
President's Organizing Fund	700.00
Officers to Meeting	2,000.00
California Filing Fee	12.50
Postage	1,650.00
Printing	350.00
Office Supplies	150.00
Postage Permit	50.00
Miscellaneous (includes telephone)	700.00
Annual Meeting Expenses	200.00
Advertisements	800.00
Memberships (WSM, ASC, etc)	120.00
Symposium Expenses (Endowment Fund Interest)	2,000.00
Student Paper Award	500.00
Treasurer's CPA Expenses	300.00
TOTAL:	$29,142.00

SUMMARY

Income	$28,825.00
Disbursements	29,142.00
Interest	2,200.00
Net	1,892.50

Donna Turgeon's report from the meeting of the Council of Systematic Malacologists held during this session included the following points:

1. The Scientific and Vernacular Names of Mollusks report, comprising some 5700 species of terrestrial, aquatic, and marine mollusks of North America from the U.S./Mexico border northward through Canada and offshore to 200 meters, but excluding islands such as Hawaii and the Virgin Islands, has been formally accepted and will be printed by the American Fisheries Society. It should be ready by the next AMU meeting. Shell Oil Company has provided a grant to publish the volume. Half of all the profits after costs will be given AMU.
2. Continued efforts to devise a National Plan will be made.
3. Work will continue to prepare a taxonomically critical list of recognized North American mollusks with abbreviated synonomies and brief geographical ranges.
4. CSM will endorse the grant application from the Bishop Museum to the Institute of Museum Services in continued efforts to help preserve the important malacological holdings at this museum.
5. The feasibility of computer net working malacological collections will be studied.
6. The desirability of a faunal survey of U.S. freshwater and terrestrial mollusks will be studied.

William G. Lyons announced that the 1987 meeting would be held at Marriott's Casa Marina Resort in Key West, Florida, July 19-23, with rooms for single or double to be $65.00 a night.

There will be a Cenozoic Mollusk Symposium conducted by Dr. Emily Vokes and a symposium on Polyplacophora led by Dr. Robert Bullock.

There will be marine, terrestrial, and freshwater field trips mid-week.

A motion to hold the 1988 meeting in Charleston, South Carolina, was approved. Richard E. Petit discussed plans to hold this meeting at the College of Charleston in the heart of this historic city. He plans symposiums on the history of malacology and DNA applications in malacology.

AMU has received $3,984.67 from the estate of Maude N. Meyer. A motion was approved as follows: "The money received from the Maude N. Meyer estate will be placed in the general fund, with the student paper award of $500.00 in 1987 to be named the Maude N. Meyer Award".

Under new business the following motions were approved:

1. The AMU Newsletter will not publish articles as an outlet of scientific research.
2. AMU will discontinue the bonus gift of bulletins to new members starting January 1, 1987. This was clarified to announce that bulletins are included in the dues year, with members due to the get the bulletins paid for by their dues. This has meant the bulletins delivered the next year.
3. The incoming President will appoint a committee to investigate the issues of reorganizing the *American Malacological Bulletin* and Newsletter and report in 1987.
4. The abstracts of the annual meeting papers will not be published in the *American Malacological Bulletin*, starting with the 1987 meeting. They will be printed in the annual meeting program, planned by the President, and using a word limit to be determined by the Publications Committee, requiring camera ready copy from speakers. The number of copies of the program printed will be determined by the President and the Publications Committee.
6. Travel funds for the Editor to attend the Unitas meeting in Scotland as an A.M.U. liaison are approved with the money to come from the *Bulletin* account.
7. AMU will contribute $250.00 to the AAZN.
8. The separate account for the *Bulletin* monies will be eliminated and *Bulletin* funds will be separated in accounting records.
9. AMU will contribute $100 to help ASC move to Washington, DC.

Adjournment came at 4:50 p.m.

Constance E. Boone, Recording Secretary

FINANCIAL REPORT

REPORT OF THE TREASURER FOR THE FISCAL YEAR ENDING DECEMBER 31, 1985

CHECK BOOK BALANCE, JANUARY 1, 1985			$6,383.00
RECEIPTS:			
Memberships:			
Regular	$12,345.50		
Sustaining	181.00		
Student (regular)	649.00		
Student (foreign)	22.50		
Corresponding	1,208.50		
Clubs	969.00		
Institutions	2,367.00		
	$17,742.50		
		17,742.50	
Sales:			
AMU BULLETIN (Back issues/Special Editions)	2,920.62		
Teskey Index	26.30		
Rare & Endangered Species	3.69		
HOW TO STUDY AND COLLECT SHELLS	271.75		
	3,222.36		
		3,222.36	
Other Receipts:			
Best Student Paper Donations	579.00		
Endowment Fund Donations	1,478.50		
1985 Auction Proceeds	954.95		
Proceeds from Kingston Meeting	5,009.55		
Endowment Fund Interest Withdrawn	1,673.25		
Interest on Life Membership	266.21		
Maude Meyer Estate	3,984.67		
Money Market Account (Transfer)	5,410.79		
Interest on Checking Account	857.99		
Miscellaneous donations	114.50		
	20,329.41		
		20,329.41	
Total Cash Receipts Accounted For	41,293.83		41,293.83
TOTAL CASH ACCOUNTED FOR			$47,676.83

DISBURSEMENTS:

AMU BULLETIN, incl. postage, printing, etc.	$6,397.28	
AMU NEWSLETTER, incl. postage, printing, etc.	1,106.28	
Other Postage	906.29	
Other Printing	397.11	
Office Supplies	106.30	
Dues and Advertising	867.50	
AMU-Kingston Tee Shirts	699.00	
Officers' Travel - Kingston	976.18	
Filing Fee (California)	12.50	
Symposium Endowment Fund Deposits	1,568.00	
Deposit URI-Kingston	1,000.00	
Deposit Monterey Aquarium	250.00	
Insurance	375.00	
Telephone	493.28	
Money Market Account (Transfer)	5,410.79	
Student Awards	500.00	
Bank Charges	56.62	
Miscellaneous/Petty Cash	601.66	
TOTAL DISBURSEMENTS FROM ALL ACTIVITIES		21,723.79
CHECK BOOK BALANCE, JANUARY 1, 1985		6,383.00
TOTAL RECEIPTS		41,293.83
TOTAL CASH		47,676.83
TOTAL DISBURSEMENTS		21,723.79
CHECK BOOK BALANCE, DECEMBER 31, 1985		25,953.04

RECAPITULATION OF ASSETS, DECEMBER 31, 1985:

Cash in Checking Account, First Independent Bank	25,953.04
Bulletin Account	18,000.00
Fortune Federal Acct. 0203127749	5,805.91
Editor's Fund	1,656.33
SASA Acct. #22-906859	3,282.64
First Independence Acct. #3600459	898.22
First Federal Acct. #6800057-02	2,758.44
First Independence Acct. #80338	11,437.74
Life Membership Account #22-906859	3,193.78
TOTAL ASSETS	$72,986.10
AMU NET WORTH, DECEMBER 31, 1985	72,986.10
CHANGES IN CAPITAL ACCOUNT:	
AMU Capital Acct., January 1, 1985	38,960.00
AMU Capital Acct., December 31, 1985	72,986.10
NET INCREASE IN ASSETS, 1985	34,025.11

Respectfully submitted,
Anne Joffe, Treasurer 1985

AMERICAN MALACOLOGICAL UNION, INC.
EXECUTIVE COUNCIL
1986 - 1987

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(Revised Nov. 1, 1986)

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KNUTSON, DR. LLOYD, Chairman, Insect Ident. and Beneficial Insect Introduction Institute, USDA, Rm. 1, Bldg. 003, Beltsville Agric. Research Center, Beltsville, MD 20705 (Study of natural enemies of molluscs (esp. Sciomygidae); biological control of pest snails).

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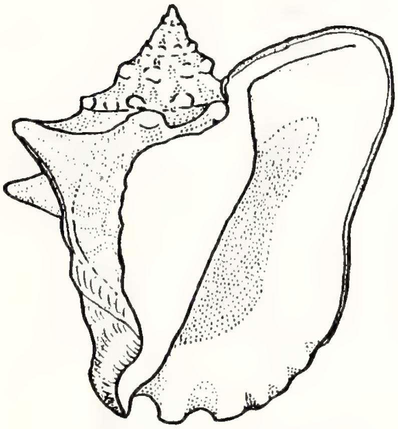

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JULY 19-23, 1987

The 53rd annual meeting of the American Malacological Union will be held July 19-23, 1987, in tropical Key West, Florida. Marriott's beachfront Casa Marina Resort offers the amenities of a grand hotel near the many charming restaurants, shops, and other attractions of the downtown area. Key West is easily accessible by air from Miami or Tampa and is served by four airlines. Travelers by land can drive to Key West via the scenic Overseas Highway.

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BIOLOGY OF THE POLYPLACOPHORA
(Organized by Robert Bullock)

In addition to the symposia, contributed papers and poster presentations, scheduled events will include a tour of historic Key West, guided field trips to the terrestrial and marine molluscan communities of the Florida Keys, an auction to benefit the symposium fund, and a banquet.

For further information please contact:
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Beattie, J. H., K. K. Chew, and W. K. Hershberger. 1980. Differential survival of selected strains of Pacific oysters (*Crassostrea gigas*) during summer mortality. *Proceedings of the National Shellfisheries Association* 70(2):184-189.

Seed, R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms*, D. C. Rhoads and R. A. Lutz, eds. pp. 23-67. Plenum Press, New York.

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Cover. Interstitial molluscs from Fiji include several species of opisthobranchs. These small gastropods are discussed in a paper by Morse (page 281) in this issue. The latter is one in a series of papers that appear herein as part of the proceedings of the 1986 American Malacological Union - Western Society of Malacologists Symposium on the Biology and Evolution of Opisthobranch Molluscs.

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June 1987

ALLOZYMIC VARIABILITY AND HETEROZYGOTE DEFICIENCY WITHIN AND AMONG MORPHOLOGICALLY POLYMORPHIC POPULATIONS OF *LIGUUS FASCIATUS* (MOLLUSCA: PULMONATA: BULIMULIDAE)

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ABSTRACT

Allozymic variability was examined within and among seven morphologically variable hammock populations of *Liguus fasciatus* (Müller). These populations contained representatives of 14 named varieties of this species; each hammock contained at least two phenotypic varieties. Among 24 gene loci examined, only one (glucose phosphate isomerase) was variable either within or among populations. These data substantiate the existence of a single polymorphic species within these populations.

Very narrow (25 m) separations of some hammocks by water represent significant barriers to gene flow between populations of *Liguus fasciatus*. However, recent woody growth between two adjacent hammocks has facilitated bidirectional immigration of snails. Reproduction between immigrant and resident snails appears to have been minimal, either because of the recent nature of the immigration or because of self-fertilization or assortative mating by the immigrants.

Most populations have significant heterozygote deficiencies at the glucose phosphate isomerase locus compared to the expectations of Hardy-Weinberg equilibrium, probably an indication of some degree of self-fertilization. The limited phenotypic combinations of shell patterns and colors present in the study populations are also not consistent with the proposed independence of a number of phenotypic characters if reproduction occurs by outcrossing. Interpretation of the inheritance of morphological characters is hampered by a lack of knowledge concerning the mode or modes of reproduction in *Liguus fasciatus*; further study of codominantly inherited allozymic alleles should facilitate such investigations.

Tree snails of the genus *Liguus* occur in southern Florida, Cuba, and Hispaniola. Currently, five species are recognized, although well over 150 trivial names are applied to various distinctive varieties (Clench, 1946, 1954, 1965; Jones, 1979). Most of the morphological and nomenclatural variability occurs in the species *Liguus fasciatus* (Müller), which occurs in Florida and Cuba (including the Isle of Pines). In Florida, approximately 58 named varieties of *L. fasciatus* occur (Roth and Bogan, 1984); these often have been divided into various numbers of subspecies (Clench and Fairchild, 1939; Pilsbry, 1899, 1912, 1946; Simpson, 1929).

Much of the morphological variation in *Liguus fasciatus* occurs among, rather than within, populations. In southern Florida, most populations are restricted to tropical hardwood hammocks isolated by water, sawgrass, buttonwood, cypress, or pine forest. In many of these populations, only one or a few phenotypes occur; furthermore, many phenotypes are restricted to single areas (Deisler, 1982).

Roth and Bogan (1984) devised a system for describing phenotypic variation in Floridian populations of *Liguus fasciatus*. They designated shells on the basis of twelve characters, each character with from two to four possible states. Roth and Bogan (1984) stated that they chose characters "...in which the alternate states can be seen to segregate in randomly selected material." Under their system, theoretically there are 33,280 possible phenotypic combinations (49,152 genotypic combinations, but 15,872 of these cannot occur as logical phenotypes, because they describe variation in bands that are not expressed). However, the vast majority of these combinations have never been reported. Roth and Bogan (1984) reported a total of 97 phenotypic combinations of *L. fasciatus* shells that have been grouped into the 58 nominal Floridian taxa. These represent 0.3% of the theoretically possible phenotypic combinations. The majority of these phenotypes are known from hundreds or thousands of museum specimens, so the absence of most phenotypic combinations is puzzling if the various characters are independent. Furthermore, in many populations, two

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phenotypes exist sympatrically that differ in numerous character states, and yet no other combinations of these states are known from the populations (Pilsbry, 1946).

One possible explanation for the above observations is that the characters described by Roth and Bogan (1984) are not independent and that entire phenotypes (or large portions of phenotypes) are under control of one or a few tightly linked gene loci. Another possiblity is that reproduction is not always accomplished through outcrossing in *Liguus fasciatus*, although mating does precede egg-laying (Brown, 1978; Jones, 1954; Pilsbry, 1946; Simpson, 1929; Solem, 1961). Even though mating occurs, reproduction could occur by gynogenesis, or mating could be required for ovulation before self-fertilization can occur. It is also possible that some phenotypes referred to the taxon *L. fasciatus* are reproductively isolated and specifically distinct. In order to discriminate among these possibilities, we examined the products of 24 enzyme loci in several morphologically variable populations of *L. fasciatus* by means of starch gel electrophoresis. Electrophoretic studies of codominantly inherited allozymes have proven to be a useful means of discriminating among reproductive modes in numerous organisms (Nevo, 1978). In addition, allozymic studies have been invaluable in determinig whether cases of morphological variation are the result of intraspecific polymorphism or reproductive isolation (see Hillis and Patton, 1982, for another example from molluscs).

MATERIALS AND METHODS

Seven populations of *Liguus fasciatus* were sampled from hammocks in the vicinity of Pinecrest, Big Cypress National Preserve, Florida (see Pilsbry, 1946, for hammock numbering system); 329 individuals were collected from these populations for allozymic analysis (Table 1). Samples were collected from throughout each hammock. All of the study populations contained at least two shell phenotypes, and one population (PC 88) contained nine named morphological varieties. Each of the varieties is described in Table 1 according to the system proposed by Roth and Bogan (1984). Some individuals classified under the *walkeri* phenotype could also be called *castaneozonatus*, depending on the degree of uniformity of the major bands. Because these two phenotypes seem to form a continuum in the study populations, the two categories were lumped under the *walkeri* class.

Initial screening of allozymic loci involved 20 to 40 individuals drawn from the various populations. Twenty-four presumptive gene loci were scored: creatine kinase (2.7.3.2), ten esterase loci (3.1.1.1), glucose phosphate isomerase (5.3.1.9), isocitrate dehydrogenase (1.1.1.42), two lactate dehydrogenase loci (1.1.1.27), two malate dehydrogenase loci (1.1.1.37), mannose phosphate isomerase (5.3.1.8), peptidase A, B, C, and S (3.4.11.13), peptidase D (3.4.13.9), and phosphoglucomutase (2.7.5.1) (Enzyme Commission numbers follow Bielka *et al.*, 1984). All individuals were then scored for variation at polymorphic loci.

Standard procedures of horizontal starch gel electrophoresis were employed (see Selander *et al.*, 1971). Snails were ground and diluted 1:1 in 0.01 M tris-0.001 M EDTA-0.001 M 2-mercaptoethanol, pH 7.5. Homogenates were centrifuged at 10,000 g for 5 min and then the supernatant was refrozen at -85°C for up to three months prior to use. Two buffer systems were used: TBE 9.1 (175.0 mM tris-17.5 mM boric acid-2.75 mM EDTA, pH 9.1) and Poulik (gel: 0.076 M tris-0.005 M citric acid, pH 8.7; electrode: 0.30 M boric acid, pH 8.2). Gels were prepared from 50% Sigma starch (lot 85F-0010) and 50% Otto Hiller electrostarch (lot 392). Gels were 12% starch for both systems. Two drops of

Table 1. Morphological characters of varieties of *Liguus fasciatus* examined and distribution of varieties within study populations. Shell phenotype characters follow Roth and Bogan (1984); C: ground color of shell (Y: yellow; W: white); B: *dryas* bands (B: brown; Y: yellow; BY: both brown and yellow; O: absent); S: spreading of *dryas* band pigment; E: vacant center of *dryas* bands (B: brown band; Y: yellow band); U: absence of one *dryas* band; M: marbling of *dryas* bands; L: sutural line (B: brown; Y: yellow; O: absent); P: peripheral line (B: brown; Y: yellow; O: absent); A: pink apex; O: pink columella; W: white suffusion; G: periostracal green lines.

	Pinecrest Hammock Co.							Shell Phenotype Characters											
Variety	1a	10	11	14	16	16a	88	C	B	S	E	U	M	L	P	A	O	W	G
aurantius	--	1	--	--	1	1	6	Y	Y	+	Y	—	—	O	O	—	—	—	+
barbouri	--	17	--	--	6	32	--	Y	BY	+	B	—	+	B	B	—	—	+,—	+
clenchi	--	--	--	--	--	--	3	Y	B	+	B	—	+	O	O	+	+	—	+
elegans	--	--	--	1	--	--	--	W	O	—	—	—	—	B	B	+	+	—	+
floridanus	--	--	--	--	--	--	5	Y	BY	+	B	—	+	B	B	—	—	—	+
livingstoni	--	5	--	--	--	--	22	W	Y	—	—	—	—	O	O	+	+	—	+
lossmanicus	--	--	12	--	--	--	47	Y	O	—	—	—	—	O	O	—	—	—	+
lucidovarius	--	--	1	--	--	--	--	W	BY	+	—	—	+	B	B	—	—	—	+
miamiensis	--	5	--	--	--	--	--	W	BY	—	—	—	+	O	O	+	+	—	+
mosieri	--	--	--	--	--	--	9	W	O	—	—	—	—	O	O	—	—	—	+
ornatus	--	--	--	--	--	--	8	Y	Y	—	—	—	—	Y	Y	+	+	—	+
roseatus	3	4	--	--	5	--	1	W	Y	—	—	—	—	Y	Y	+	+	—	+
testudineus	--	--	--	--	--	--	1	Y	B	+	B	—	+	B	B	+	+	—	+
walkeri	27	20	--	40	44	2	--	W	BY	—	B,—	—	+	B	B	+	+	+,—	+

2-mercaptoethanol were added to the gel mixture after boiling and degassing. Gels were electrophoresed for 10 to 14 hr at 12.5 V/cm. Histochemical staining procedures followed Harris and Hopkinson (1976), Siciliano and Shaw (1976), and Selander *et al.* (1971).

RESULTS

All of the loci examined were monomorphic for a single allele except for the glucose phosphate isomerase locus. Two alleles were present at this locus and were designated fast (F) and slow (S). Five of the populations (PC 10, 14, 16, 16a, and 88) were polymorphic for these two alleles, whereas the other two populations (PC 1a and 11) were fixed for the fast allele (Table 2).

Genetic distances (Hillis, 1984) between populations ranged from 0 to 0.03; genetic distances between varieties pooled across populations ranged from 0 to 0.04. Among populations polymorphic for glucose phosphate isomerase, observed frequencies of the heterozygous genotype were consistently lower than predicted for populations in Hardy-Weinberg equilibrium (Fig. 1). Deviations from Hardy-Weinberg equilibrium were significant in four of the five populations PC 10: $\chi^2 = 39.30$, df = 1, $p < 0.001$; PC 14: $X^2 = 20.22$, df = 1, $p < 0.001$; PC 16: $\chi^2 = 7.36$, df = 1, $p < 0.01$; PC 16a: $\chi^2 = 24.61$, df = 1, $p < 0.001$). Average individual heterozygosity ranged from 0 in PC 1a and 11 to 0.016 in PC 88.

Table 2. Genotypes for glucose phosphate isomerase of *Liguus fasciatus* by population and variety.

Population	Variety	Genotype FF	Genotype FS	Genotype SS
PC 1a	*roseatus*	3	--	--
PC 1a	*walkeri*	27	--	--
PC 10	*aurantius*	1	--	--
PC 10	*barbouri*	1	1	15
PC 10	*livingstoni*	--	--	5
PC 10	*miamiensis*	--	1	4
PC 10	*roseatus*	--	--	4
PC 10	*walkeri*	5	--	15
PC 11	*lossmanicus*	12	--	--
PC 11	*lucidovarius*	1	--	--
PC 14	*elegans*	1	--	--
PC 14	*walkeri*	14	6	20
PC 16	*aurantius*	--	--	1
PC 16	*barbouri*	4	1	1
PC 16	*roseatus*	--	1	4
PC 16	*walkeri*	7	14	23
PC 16a	*aurantius*	1	--	--
PC 16a	*barbouri*	30	1	1
PC 16a	*walkeri*	--	--	2
PC 88	*aurantius*	1	2	3
PC 88	*clenchi*	1	1	1
PC 88	*floridanus*	--	5	--
PC 88	*livingstoni*	2	6	14
PC 88	*lossmanicus*	6	17	24
PC 88	*mosieri*	2	5	2
PC 88	*ornatus*	1	4	3
PC 88	*roseatus*	--	1	--
PC 88	*testudineus*	--	--	1

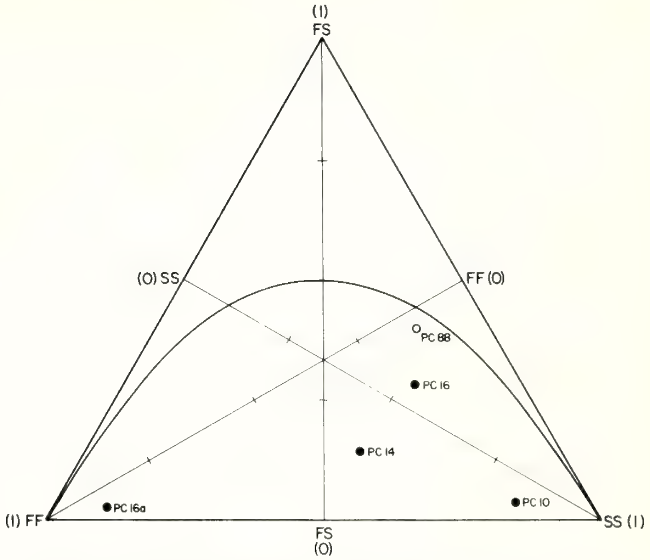

Fig. 1. Genotypic frequencies of populations of *Liguus fasciatus* variable at the glucose phosphate isomerase locus. Each of the three axes starts on one side of the triangle at a frequency of 0 and ends in a corner at a frequency of 1.0. The curve represents expected genotypic frequencies of populations in Hardy-Weinberg equilibrium. Populations represented by solid dots have a significant deficiency of heterozygous individuals ($p < 0.01$); the single population represented by an open dot does not differ significantly from Hardy-Weinberg expectations ($p > 0.05$).

DISCUSSION

Allozymic variation among morphotypes and populations of *Liguus fasciatus* is surprisingly low. The level of polymorphic loci per population in *L. fasciatus* (0 – 0.04) is lower than any other gastropod reported (Nevo, 1978), except for several self-fertilizing species (Selander and Kaufman, 1973a, b; McCracken and Selander, 1980). This is especially surprising because the normally highly polymorphic esterases and peptidases were included in this study. This low level of genetic differentiation clearly substantiates that the various phenotypes of *L. fasciatus* included in this study are conspecific.

Despite the low levels of genetic variability in *Liguus fasciatus* populations, variation at the glucose phosphate isomerase locus indicates that the water barriers between the hammock populations (Table 3) represent effective impediments to gene flow. With the exception of the two fixed populations (PC 1a and 11), all populations are significantly different in genotypic ratios at this locus (Fig. 1). Even very short water barriers appear to effectively isolate populations; for instance, PC 16 and 16a, separated by a narrow strip of water approximately 25 m wide (Table 3), support *L. fasciatus*

Table 3. Distances between hammocks in meters across water/sawgrass barriers.

	Pinecrest hammock number						
PC #	1a	10	11	14	16	16a	88
1a	----	950	1600	600	900	1050	4900
10		----	500	700	700	700	5900
11			----	1800	1900	2000	5800
14				----	45	250	5400
16					----	25	5600
16a						----	5750
88							----

populations that are significantly different in both phenotypic frequencies of the shells (Table 1) and genotypic frequencies at the glucose phosphate isomerase locus (Table 2). However, in this case there is some evidence of gene flow. In PC 16, shells are mostly of the *walkeri* phenotype (79%), with some *barbouri* (11%), *roseatus* (9%), and *aurantius* (1%) phenotypes. In contrast, PC 16a supports mostly *barbouri* (91%), with some *walkeri* (6%) and *aurantius* (3%). At the glucose phosphate isomerase locus, the S allele is dominant in PC 16, whereas the F allele is dominant in PC 16a (Table 2). For each phenotype except *barbouri* in PC 16, the dominant genotype is SS, whereas for *barbouri* it is FF (Fig. 2). Likewise, for each phenotype except *walkeri* in PC 16a, the dominant genotype is FF, whereas for *walkeri* it is SS (Fig. 2). In the 1930's and 1940's, the *barbouri* phenotype was not found in PC 16, and the *walkeri* phenotype was absent from PC 16a; dispersal apparently was occurring by the late 1970's, after some woody vegetation had grown up between the two hammocks (A. Jones, pers. comm.). This dispersal appears to have resulted in an influx of F alleles into PC 16 and S alleles into PC 16a (Fig. 2). Although dispersal by humans cannot be ruled out, it is likely that this represents natural dispersal, perhaps during periods of lowered water levels.

The genotypes of the suspected immigrant individuals in PC 16 and 16a are representative of their populations of origin (Fig. 2). Therefore, either these individuals represent first generation dispersals or the immigrants are mating preferentially among themselves (including the possibility of self-fertilization). The lack of observed genotypic differentiation among morphotypes in other hammocks reduces the likelihood of assortative mating.

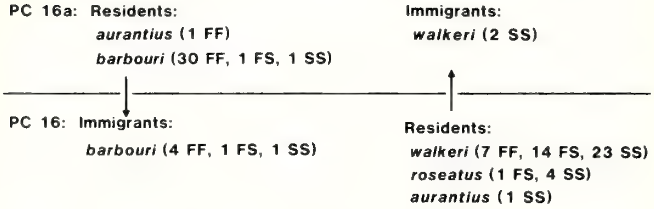

Fig. 2. Morphological phenotypes and glucose phosphate isomerase genotypes of resident and hypothesized immigrant *Liguus fasciatus* in hammocks PC 16 and 16a.

Although no studies have been conducted for confirmation, most investigators have assumed that individuals of *Liguus fasciatus* are obligate outcrossers. Clench (*In:* Young, 1960) and Brown (1978) considered parthenogeneis and self-fertilization to be unlikely in *Liguus*, for unspecififed reasons. The considerable deficiency of heterozygous individuals (Fig. 1), however, is indicative of some other mode other than outcrossing. Among other gastropods studied, degree of allozymic variation has been shown to be a strong indicator of the type of breeding system employed by the species. Among outcrossing gastropods, the percent of polymorphic loci and average individual heterozygosity are high, whereas in self-fertilizing species, average individual heterozygosity is very low and polymorphic loci are rare or absent (Selander and Kaufman, 1973a, b; McCracken and Selander, 1980). This pattern has also been observed in several other groups of hermaphroditic organisms (Brown, 1979; Harrington and Kallman, 1968; Nevo, 1978). The low levels of polymorphic loci in *L. fasciatus* (0 – 0.04) and the significant deficiencies of heterozygotes in four of five polymorphic populations are typical of self-fertilizing species. However, in one population (PC 88), there is no significant heterozygote deficiency ($\chi^2 = 1.11$, df = 1, $p > 0.05$). Several other pulmonates have been shown to consist of both self-fertilizing and outcrossing populations, or individuals may be facultatively self-fertilizing; furthermore, reproduction following copulation in *Philomycus* spp. can be either by self-fertilization or outcrossing (McCracken and Selander, 1980). The patterns of allozymic variability observed in this study indicate that multiple reproductive modes can be possible in populations of *L. fasciatus* as well.

A. Jones (pers. comm.) has made numerous introductions of *Liguus* into hammocks otherwise free of these snails. He has found that reproduction only occurs if two or more snails are introduced; single *Liguus* do not reproduce in isolation. These observations suggest that mating is essential for reproduction, but do not necessarily indicate outcrossing. Some reproduction could be by gynogenesis, in which spermatozoa from another individual are needed to stimulate embryonic development but make no genetic contribution. Alternatively, mating could stimulate ovulation, after which reproduction could be accomplished by self-fertilization. In either case, reproduction must include some outcrossing, because intermediate shells have been reported after a few generations of crosses of phenotypically distinct shells (Young, 1960).

Past attempts to study reproduction and inheritance in *Liguus fasciatus* have centered on morphological variation. However, until the potential reproductive modes of *L. fasciatus* are determined, analysis of inheritance of morphological variation will be hampered. The glucose phosphate isomerase locus, with two codominantly expressed alleles, provides a valuable tool for determining the mode or modes of reproduction in *L. fasciatus* populations. After this information is obtained, study of inheritance of morphological variation will be greatly facilitated.

In all of the study populations, it is clear that the morphological characters defined by Roth and Bogan (1984) are not randomly segregating (Table 1). Instead, they exist as discrete combinations. Several of the characters always covary in these populations (e.g. characters L and P; also characters A and O; see Table 1). If the characters specified by Roth and Bogan (1984) are independent, then reproduction must be by self-fertilization or some form of parthenogenesis in these populations. Alternatively, the shell phenotypes of *Liguus fasciatus* could be specified by fewer loci than has been proposed.

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THE FUNCTIONAL MORPHOLOGY OF THE ORGANS OF THE MANTLE CAVITY OF *PERNA VIRIDIS* (LINNAEUS, 1758) (BIVALVIA: MYTILACEA)

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ABSTRACT

In Hong Kong and throughout its large geographic range, the epibyssate mussel *Perna viridis* (Linnaeus) tolerates widely varying hydrographic regimes. Obvious physiological adaptations are matched by appropriate interpopulation variations in life history characteristics.

This study of feeding structures and mechanisms in the mantle cavity reveals other, morphological, adaptations. Ctenidial collection areas are relatively small. Similarly, the sorting areas of the labial palps are small and the dorsal edges of the palps are extensively fused to either the visceral mass or the mantle so that they rigidly project backwards into the mantle cavity and are thus intimately apposed to the ctenidia. The anterior ends of the ctenidia and the sorting areas of the palps are mostly rejectory. Although of the basic mytilid form, the arrangement of the feeding organs, and their ciliary currents, reveals how *Perna viridis* is particularly able to occupy waters with high sediment loadings. The efficiency of particle rejection suggests that high turbidities do not limit the distribution of *P. viridis.* Such adaptations, together with other physiological and reproductive adaptations, account for the dominance of this species in tropical estuarine and other marine environments.

The genus *Perna* is represented by three species having non-overlapping geographic ranges. *P. canaliculus* (Gmelin) is restricted to New Zealand, *P. perna* (Linnaeus) is widely distributed along the coasts of Africa and the Atlantic coasts of South America while *P. viridis* (Linnaeus) is Indo-Pacific (Siddall, 1980). *P. viridis* is widely distributed within the Indo-Pacific, having a western limit at the Persian Gulf and an eastern limit at New Guinea. It has not been recorded south of New Guinea and Habe (1977) considers southern Japan to be its northern limit. Interestingly, Siddall (1980) does not consider *P. viridis* to be naturally distributed along the coast of China or Japan and Arakawa (1980) believes the species was introduced into Japan sometime around 1967. Possibly, therefore, the species has been introduced into Hong Kong also. Irrespective of this, *P. viridis* is a dominant feature of many hard intertidal and subtidal habitats in Hong Kong.

The distribution of *Perna viridis* in Hong Kong waters has been reported upon by Huang *et al.* (1985). Hong Kong can be divided longitudinally into three hydrographic zones (Fig. 1): a western estuarine zone, greatly under the influence of the Pearl River, is characterised by fluctuating low salinities and high sediment loadings; an eastern zone, in which shores are exposed to predominately oceanic waters and a central transition zone where western and eastern waters meet and the water column is stratified (Morton, 1982, 1985).

Transition zone waters are also typical "harbour" waters encompassing two important harbours, Victoria and Tolo. *Perna viridis* can be found throughout Hong Kong's waters, excluded only from areas experiencing extremely low salinities as at Tsim Bei Tsui in Deep Bay in the northwestern quadrant of Hong Kong and from the exposed reaches in the southeastern quadrant of Hong Kong. Figure 1 summarises distribution data and shows that highest densities (>200 adult individuals m^{-2}) are consistently recorded from Victoria and Tolo Harbours. Lower densities (<100 m^{-2}) are recorded from eastern and western waters. Huang *et al.* (1985) explain the local distribution of *P. viridis* by suggesting that the consistently low salinities ($<5^{0}/_{00}$) in the west and exposure to wave action in the east limit establishment and growth. Lee and Morton (1985) consider that the wide distribution implies successful adaptation to a broad range of hydrographies, but that differences in densities reflect water quality preferences. *P. viridis* is most abundant in Victoria and Tolo Harbours where the water is polluted by domestic, agricultural and industrial effluents (Morton, 1982, 1985). Lee (1985) has shown that in

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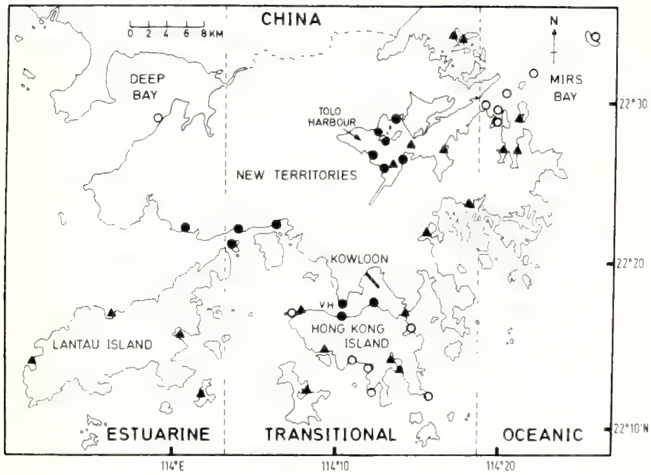

Fig. 1. The distribution of *Perna viridis* in Hong Kong, in relation to broadly recognised hydrographic zones (After Huang *et al.*, 1985) (Solid circles, density >100 m^{-2}; triangles, density <100 m^{-2}; open circles, *P. viridis* not found).

Victoria Harbour, *P. viridis* shows retarded growth rates, precocious mortality and low tissue weights. Despite these pollution induced stresses, *P. viridis* dominates the epifaunal community by virtue of physiological tolerances and a restricted breeding season. In other parts of Hong Kong, where the species is less numerous, it grows faster, lives longer, has greater tissue weights and breeds year round, so that here too the species is a significant feature of the epifaunal community.

Apart from descriptions of the shell, e.g. Siddall (1980), there is no comprehensive morphological study of *Perna viridis.* This study investigates the functional morphology of the organs of the mantle cavity of *P. viridis*, to determine if there are anatomical and functional characteristics that supplement physiological and life history characteristics permitting the exploitation of a wide range of habitats.

MATERIALS AND METHODS

Specimens of *Perna viridis* were obtained from the pier at Wu Kwai Sha, Tolo Harbour, New Territories of Hong Kong in March 1986. Following dissection, ciliary currents were elucidated using fine grade carborundum and powdered milk. For histological purposes, specimens were fixed in Bouin's fluid, decalcified, sectioned at 6 μm and alternate slides stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome.

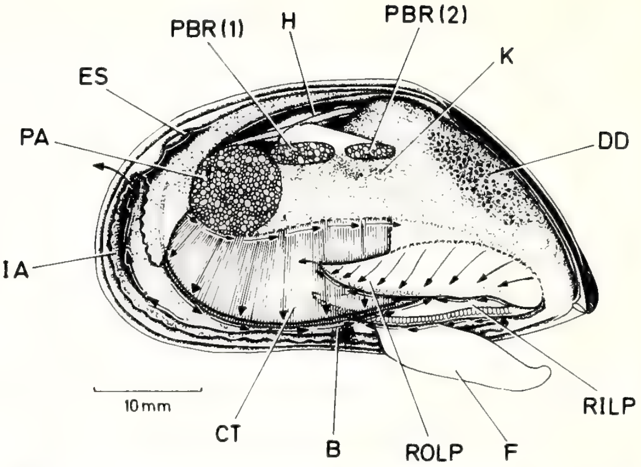

Fig. 2. *Perna viridis.* The animal as seen from the right side and after removal of the right shell valve and mantle lobe. Ciliary currents are indicated by arrows [B, byssus; CT, ctenidium; DD, digestive diverticula; ES, exhalant siphon; F, foot; H, heart; IA, inhalant aperture; K, kidney; PA, posterior adductor muscle; PBR(1) and PRB(2), components of the posterior byssal retractor muscle; RILP, right inner labial palp; ROLP, right outer labial palp].

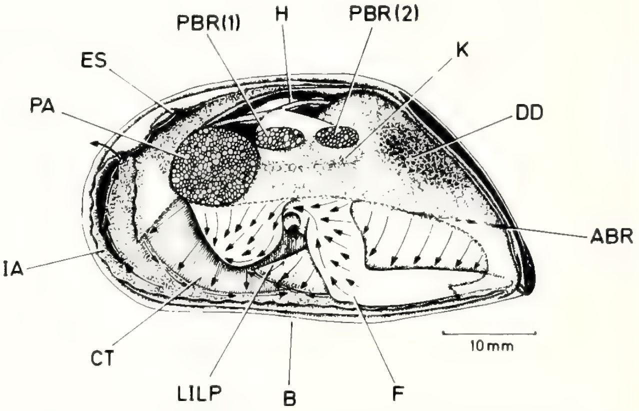

Fig. 3. *Perna viridis.* The animal as seen from the right side and after removal of the right shell valve, mantle lobe, right ctenidium and right labial palps to show the ciliary currents of the visceral mass [ABR; anterior byssal retractor muscle; B, byssus; CT, ctenidium; DD, digestive diverticula; ES, exhalant siphon; F, foot; H, heart; IA, inhalant aperture; K, kidney; LILP, left inner labial palp; PA, posterior adductor muscle; PBR(1) and PBR(2), components of the posterior byssal retractor muscle].

FUNCTIONAL MORPHOLOGY

Perna viridis is mytiliform, with extreme reduction of the anterior but expansion of the posterior faces of the shell and ventral flattening (Fig. 2). Although the form of *P. viridis* is not so extreme as open-coast mytilids, e.g. *Septifer* (Yonge and Campbell, 1968), with ventral flattening such that the greatest shell width is basal, an unusual feature is the absence of an anterior adductor muscle, i.e. *P. viridis* is monomyarian (as are other species of the genus). The posterior adductor muscle is large (Fig. 2: PA), as is the posterior byssal retractor muscle which is divided into two components [PBR (1), PBR(2)]. The anterior byssal retractor (Fig. 3: ABR) is small and located posterior to the umbones, below the ligament.

THE MANTLE

Mantle fusion only occurs between the inhalant and exhalant apertures. The latter is conical (Figs. 2, 3: ES), the former (IA) long and without the sensory papillae typical of other mytilids, e.g. *Mytilus* (Soot-Ryen, 1955) and *Xenostrobus* (Wilson, 1979). The mantle is variably patterned dark brown, but usually with a darker stripe decorating each side of the outer surface of the exhalant siphon and the inner surfaces of the inhalant aperture. The mantle contains much of the gonad and the ventral mantle margin, seen in transverse section in Figure 4, comprises the usual three folds (Yonge, 1957, 1982): inner (IMF), middle (MMF) and outer (OMF). The outer and middle folds are of the typical plan and fulfill typical functions (Yonge, 1983). Of interest, however, is the inner fold which is greatly enlarged and divided into two components; inner [IMF(I)] and outer [IMF(O)]. The inner component has an extensive haemocoel and probably can be inflated with blood. Between it and the general mantle surface is a deep, densely ciliated, rejectory tract (RT). The outer component of this fold is secretory and possesses a large sub-epithelial gland (MG), the basiphilic cells of which are some 20 μm in diameter. It is believed that these glands, along with other glands in the foot (not illustrated), produce the copius amounts of mucus that are characteristic of *Perna viridis*.

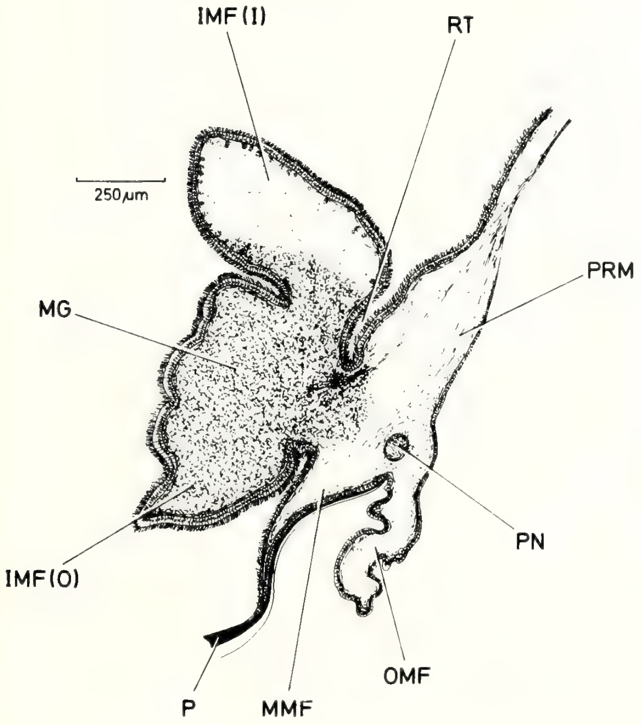

Fig. 4. *Perna viridis.* A transverse section through the right mantle margin at the pedal gape and showing the extent of the mucous gland (MG) in the outer component of the inner mantle fold [IMF(O)], [IMF(1), IMF(2), inner and outer components of the inner mantle fold; MG, mucous gland; MMF, middle mantle fold; OMF, outer mantle fold; P, periostracum; PN, pallial nerve; PRM, pallial retractor muscle; RT, rejectory tract].

THE CTENIDIA

Unlike the majority of bivalves where the larger proportion of the mantle cavity is located lateral to the visceral mass, that of the Mytilacea, including *Perna viridis*, is largely beneath the body in the expanded ventral component of the shell.

The ctenidia are generally typical of the Mytilacea and are flat, homorhabdic, non-plicate, filibranch and comprise approximately equal inner and outer demibranchs (Figs. 2, 3). The gill ciliation is of type B(1) (Atkins, 1937). The ctenidia are removed from the anteriormost apex of the shell and the anterior filaments of the ctenidia are unusually arranged. In the boring mytilid *Adula falcata* (Gould), Fankboner (1971) showed that the outer demibranchs are typically some 10 filaments shorter at their anterior ends than the inner demibranchs. Material arriving at the ctenidial-labial palp terminus on the outer demibranch, therefore, must pass onto the inner demibranch before proceeding to the palps and mouth. Similar situations exist in other mytilids, e.g. *Limnoperna, Musculista, Modiolus* and *Arcuatula* (Morton, 1973, 1974, 1977a, b, 1980). This is not the case in *Perna viridis.* Anteriorly (Figs. 5, 6), the demibranchs (ID; OD) are of the same length, but particles arriving at the terminus in the ventral margin food groove of the outer demibranchs stop about 14 filaments from the end. Moreover, the cilia in the ventral marginal food groove of the anteriormost 14 filaments, beat posteriorly so that the two streams meet and from this point (Figs. 5, 6: star) transported particles can fall onto the palps (RILP, ROLP) for resorting.

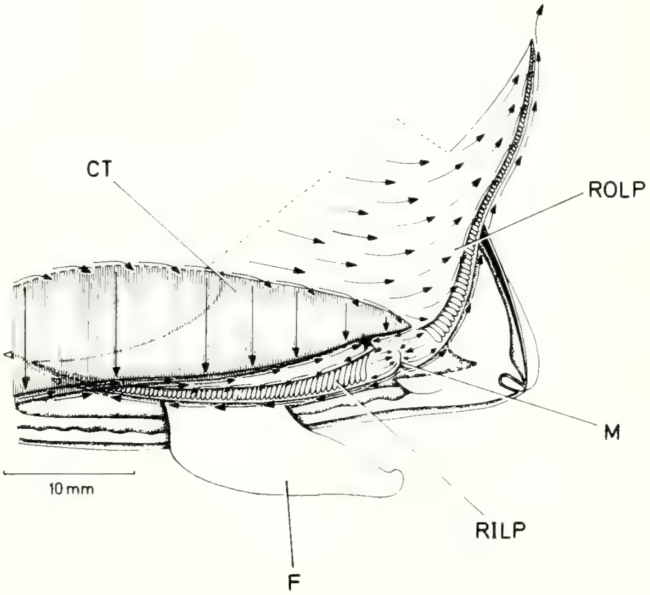

Fig. 5. *Perna viridis.* A detail of the anterior region of the body, after removal of the right shell valve and mantle lobe and showing the ciliary currents of the anterior half of the ctenidium and palps in greater detail. The star identifies where ctenidially collected particles fall onto the palps (CT, ctenidium; F, foot; M, mouth; RILP, right inner labial palp; ROLP, right outer labial palp).

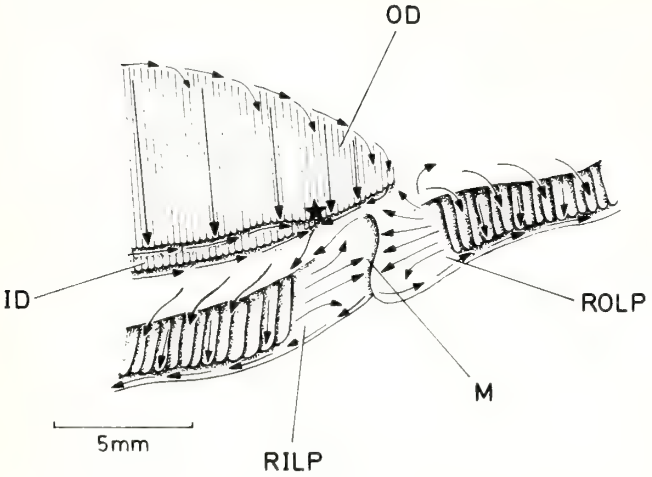

Fig. 6. *Perna viridis.* A further detail of the anterior region of the ctenidium and labial palps showing the ciliary currents. The star identifies where ctenidially collected particles fall onto the palps (ID, inner demibranch; M, mouth; OD, outer demibranch; RILP, right inner labial palp; ROLP, right outer labial palp).

THE LABIAL PALPS

The unusual ctenidial terminus of *Perna viridis* is matched by equally unusual palps. As might be expected from an inhabitant of turbid waters, the labial palps are both large and long (Fig. 2: RILP, ROLP), reaching backwards for some half of the length of the mantle cavity. Unlike other bivalves, especially other mytilids, however, the dorsal edges of the palps are united with either the mantle or the visceral mass, for more than two-thirds of their lengths. In the case of the outer demibranch, union is with a flap of the mantle (Fig. 2), while in the case of the inner palps, union is with the visceral mass at a point just below where the palp attaches to the ascending lamella of the inner demibranch (Fig. 5). In addition, the sorting area of each palp is small, restricted to a thin line of ridges along the inner ventral margin (Figs. 5, 6). The large naked surfaces of the inner and outer faces of both inner and outer palps bear strong ciliary currents which pass material downwards and backwards towards the tips of the palps. Some of this material passes onto the filaments of the inner ventral margin of the palp, but the great majority quickly flows over the ridges to the ventral edge where a strong rejectory tract also passes this to the palp tips. The great majority of material arriving at the ctenidial terminus is therefore quickly rejected.

The ciliary currents of the palp ridges have been examined in detail (Fig. 7). In the grooves between each ridge, material is passed downwards (VI, VIII) to contribute to a major rejectory tract in the depths of the grooves (VII). The crests of the grooves are characterised by acceptance and resorting currents. Passing orally over the crests of the palps are extraordinarily weak acceptance tracts (I, III). In fact, unlike the majority of bivalves where the acceptance tracts are powerful, creating a major flow, it is difficult to discern such currents in *Perna viridis*. Also on the crests of each ridge is a resorting current (II) passing material towards the ventral edge of the palp. On the oral face of each ridge are cilia transporting material down into the groove (I), while on the aboral face, opposing currents (III, V) take material out of the groove. On both faces are longitudinal resorting currents (IV, IX), transporting material dorsally, away from the ventral rejectory tract.

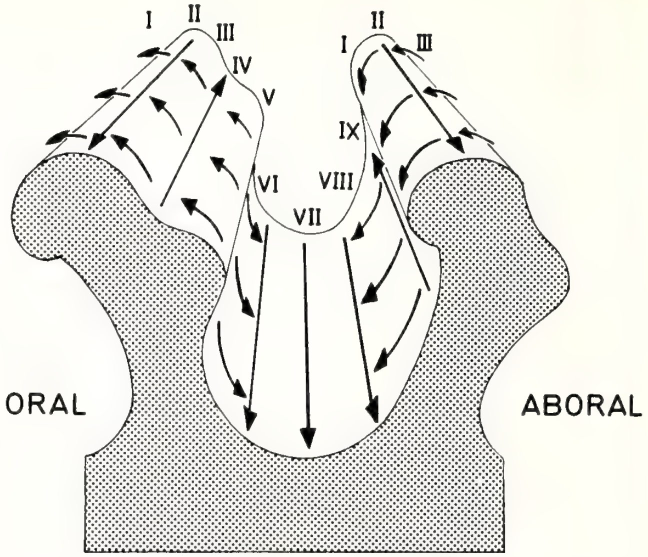

Fig. 7. *Perna viridis.* A diagrammatic representation of two ridges of a labial palp to show the various ciliary tracts [For explanation of Roman numerals see text, but note that there is no powerful acceptance tract sweeping particles over the palp crests as in other mytilids, e.g. *Modiolus metacalfei* Hanley (Morton, 1977a: Fig. 8)].

The palp ridges, therefore, are of typical mytilid form, possessing an array of acceptance, resorting and rejection tracts. The first of these functions is, however, severely reduced and the palps largely fulfill a rejectory or cleansing role.

THE FOOT AND CILIARY CURRENTS OF THE VISCERAL MASS AND MANTLE.

The foot (Figs. 2, 3: F) is of the typical mytilid form, long, highly mobile and plantar. At rest, it projects into the anteriormost reaches of the mantle cavity, a small hook-like distal swelling positioning it behind the anterior lip of the mouth (Fig. 3).

The foot, as in most bivalves, bears few ciliary tracts. The dorsal regions of the foot and the visceral mass, however, bear powerful ciliary currents which pass material postero-dorsally and then postero-ventrally to the posterior edge of the visceral mass where the material falls onto the mantle below (Fig. 3).

The ciliary currents of the mantle are similarly rejectory. On the general surface of the mantle, material is passed downwards and backwards on each lobe to accumulate in a deep posteriorly directed, rejection tract (Fig. 4: RT), on the inner mantle margin. Such material, in the form of a mucus-bound pseudofaecal string, is passed posteriorly towards the inhalant aperture. Here such material is passed dorsally and is eventually rejected from the dorsal edge of the inhalant aperture (Figs. 2, 3) as is typical of the Mytilacea (Morton, 1973).

DISCUSSION

Throughout its broad range, *Perna viridis* has been reported to have a phenomenal growth rate of some 10 mm per month, so that a marketable size of rope-cultured individuals is achieved within six months. Comparative growth rates for Goa, Johore Straits, the Philippines and Penang are 8, 10, 9 and 10 mm per month, respectively (Choo, 1974; Rao *et al.,* 1975; Qasim *et al.,* 1977; Cheong and Chen, 1980; Walker, 1982).

In waters of different quality, *Perna viridis* either exhibits continuous breeding and spat recruitment, as in the Johore Straits (Tham *et al.,* 1973; Choo, 1974) and Quezon, Philippines (Walter, 1982), or reproduction centres around two peaks in March-April and October-November (Rao *et al.,* 1975; Sivalingham, 1977). The differences in water quality which are responsible for such a reproductive dichotomy also expose the animal to different physiological stresses. *P. viridis*, like its European counterpart, *Mytilus edulis* (Linnaeus), appears to be generally adapted to the variable physiochemical environment of the low intertidal of estuaries (and harbours) (Davenport, 1983). This author has demonstrated that *P. viridis* has a greater tolerance of reduced salinities than *M. edulis* and that ciliary rates of *P. viridis* are maximal between temperatures of 32-36ºC, as compared with 25-32ºC for *M. edulis. P. viridis* is also capable of surviving prolonged emersion by aerial respiration which *M. edulis* does not (Davenport, 1983). Importantly, *P. viridis* tolerates very high turbidities in locations where it is most abundant, i.e. the Straits of Johore (Cheong and Chen, 1980), Penang, Malaysia (Choo, 1974), the Ennore estuary, Madras (Shafee, 1979), Thailand (Chonchuenchob *et al.,* 1981) and Hong Kong (Huang *et al.,* 1985; Lee, 1985; Lee and Morton, 1985).

With such growth rates, high fecundity and physiological tolerance to fluctuating estuarine environments, it seemed to this author that *P. viridis* could possess unusual morphological adaptations that allow it to cope with particularly high sediment loads. On the basis of the above observations it is clear that nutrient supply to *P. viridis* is unlikely to be limiting and that the animal is more likely to be morphologically adapted to removing sediment. This is so, but importantly, the adaptations are different from those possessed by deposit feeding bivalves of soft muds. In the infaunal Tellinacea, for example, the ctenidia are typically small, while the palps and their sorting ridges are respectively large and extensive (Yonge, 1949). Similarly in members of the Solenacea, e.g. *Sinonovacula* (Morton, 1984) and *Orbicularia* (Purchon, 1984), the same generalisation holds true. On the other hand, the mangrove anomiid, *Enigmonia aenigmatica* (Holton), though living in highly turbid waters such as the Straits of Johore, where *P. viridis* also occurs, has small labial palps with ciliary tracts that are wholly acceptance oriented. Sorting, in addition to collection, is effectively the role of the ctenidia (Morton, 1976). Clearly different bivalves have different ways of handling highly turbid inhalant water.

For the Mytilidae, ctenidia and palp structure and size have been considered to be relatively uniform (Fankboner, 1971). The ctenidia are ventral, as opposed to lateral, in position and the palps long and strap-like and divided into two components: a dorsal unridged area and a ventral region of strong ridging, e.g. *Septifer* (Yonge and Campbell, 1968), *Adula* (Fankboner, 1971), *Limnoperna, Musculista, Modiolus* and *Arcuatula* (Morton, 1973, 1974, 1977a, b, 1980). In addition, the anterior extent of the outer demibranch is shorter than that of the inner, the ctenidial-labial palp junction being diagnostic for the family (Fankboner, 1971). These generalisations are not so applicable to *Perna viridis*. Both demibranchs are of equal length, but with transport of material along the food grooves to a point about 14 filaments from the anterior end of the ctenidium. Anterior to this, particles move posteriorly along the food grooves to this point. Similarly, although the palps are relatively enormous, they have only a small ventral sorting area and further that although an usual array of acceptance, resorting and rejection tracts on the ridges and grooves are present, the acceptance tracts are so weak as to be just detectable. Moreover, by fusion with the mantle and visceral mass, the palps are not freely mobile as in other bivalves, but firmly project backwards into the mantle cavity, enforcing apposition with the ctenidia. *P. viridis* also secretes copious amounts of mucus from extensive glands within the foot and along the entire length of the mantle margin contained within a specialised sub-fold of the inner mantle fold. Finally, there are strong rejectory tracts in the mantle margins and on the visceral mass.

The organs of the mantle cavity of *P. viridis* are adapted for the rejection of considerable quantities of sediment. Material in the inhalant water is thickly bound up with mucus and, in the anterior regions of the mantle cavity, virtually all surfaces are concerned with rejection of these mucus-bound strings of particulate material. Probably only the finest particles are accepted. The adaptations shown by *P. viridis* are wholly different from those of other bivalves inhabiting turbid waters and, moreover, represent a significant deviation from the standard mytilid plan. Common mytilid features, such as the ventral mantle cavity, strap-like palps and dorsoventrally narrow ctenidia relate to the evolution of the heteromyarian form (*P. viridis* is, however, monomyarian), particularly in connection with the reduction of the anterior component of the mantle cavity. The peculiar adaptations noted above, however, clearly relate to the success of *P. viridis* in turbid tropical estuarine waters and complement physiological and reproductive adaptations.

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THE PREHISTORIC FRESHWATER MUSSELS (NAIADES) FROM BROGLEY ROCKSHELTER IN SOUTHWESTERN WISCONSIN

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ABSTRACT

This report considers nearly 6,000 freshwater mussel valves representing 25 species from the Brogley Rockshelter, a prehistoric Indian site adjacent to a small river in southwestern Wisconsin's Driftless Area. The majority of valves from Brogley are divisible into two component assemblages, one datable to circa 2800-1 B.C. and the other A.D. 1-1200. These assemblages, characterized by a complex of small river/stream taxa, are unlike modern naiad communities known in the region and add to our knowledge of prehistoric naiad zoogeography. It is suggested that poor habitat conditions resulting from early Twentieth Century land use led to the demise of most small river mussel communities in the Driftless Area.

The distribution of freshwater mussel (Mollusca: Bivalvia:Unionidae) taxa during historic times is fairly well known in those portions of the Mississippi River (e.g. Baker, 1928; Van der Schalie and Van der Schalie, 1950; Havlik and Stansbery, 1978; Thiel, 1981) and the Wisconsin River (Baker, 1928; Mathiak, 1979; Stern, 1983) that cross southwestern Wisconsin's unglaciated "Driftless Area". The smaller, interior rivers of this region; however, have received little malacological attention and are considered to be poor habitats for mussels as a result of severe historic flooding (Mathiak, 1979). The prehistoric mussel valves recovered at Brogley Rockshelter make it clear that at least some of the region's smaller rivers once contained abundant and taxonomically diverse communities of freshwater mussels.

Research on Holocene (post-glacial) stream valley deposits in the Driftless Area has documented long-term fluctuations in flood magnitudes with periods of destabilization that resulted in "large-scale erosion and reworking of valley-floor sediments, including the flushing of stored sediments from many valleys" (Knox, 1985). It is probable that pre-European Holocene mussel communities established in Driftless Area streams and small rivers would experience stress and perhaps local extirpation due to cyclical destabilization of stream beds. Although mussel populations have recently been located living in some Driftless Area small rivers, these are depauperate in species diversity when compared to similar sized streams bordering this region (Mathiak, 1979). The poor representation of modern mussel populations in the smaller rivers of the Driftless Area seems attributable to a combination of factors, but particularly devastating would have been the extreme flooding and high sediment loads brought about by "abusive land use" practices during the early Twentieth Century (Knox, 1985). The adverse effect to most mussel taxa from severe substratum disruption, sediment in prolonged suspension or silt deposition has been widely recognized (Baker, 1928; Ellis, 1936; Van der Schalie and Van der Schalie, 1963; Parmalee, 1967; Stansbery, 1970; Fuller, 1980a; Marking and Bills, 1980; Oesch, 1984).

METHODS AND MATERIALS

The freshwater mussel valves recovered at Brogley Rockshelter are housed at the University of Wisconsin-Madison, Department of Anthropology, where they were studied. The species represented, total number of valves, minimum number of individuals (MNI), and the relative abundance (%) of each species is presented in Table 1. The MNI was determined by the maximum number of right or left valves of each naiad species present in the Brogley Rockshelter components (see Table 2).

The naiad taxonomy used in this report follows the nomenclature presented by Stansbery (1982) and employed by Oesch (1984). (Oesch's work offers selected commentary from Stansbery on taxa having controversial nomenclature.) A series of voucher specimens for each species represented in the Brogley Rockshelter, Preston Rockshelter, Millville site and modern Grant River assemblages are on deposit at the Ohio State University, Museum of Zoology (OSUM). The use

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Table 1. Freshwater mussels identified at Brogley Rockshelter by component.

	Woodland Component A.D. 1-1200			Archaic Component 2800-1 B.C.			Unproveni-enced			Site Total		
Family Unionidae	Valves	Indiv.	%	Valves	Indiv.	%	Valves	Indiv.	%	Valves	Indiv.	%
Subfamily Anodontinae												
Anodonta grandis s.l.	6	5	.50	14	8	.76	8	4	.39	28	17	.55
Anodontoides ferussacianus (Lea)	0	0	0	5	3	.29	1	1	.10	6	4	.13
Strophitus undulatus undulatus (Say)	61	33	3.29	66	35	3.33	34	20	1.94	161	88	2.85
Alasmidonta marginata Say	36	23	2.29	23	14	1.33	39	21	2.04	98	58	1.88
A. viridis (Rafinesque)	12	6	.60	2	2	.19	14	9	.87	28	17	.55
Arcidens confragosus (Say)	0	0	0	0	0	0	1	1	.10	1	1	.03
Lasmigona complanata (Barnes)	0	0	0	1	1	.10	0	0	0	1	1	.03
L. costata (Rafinesque)	20	10	1.00	22	16	1.52	16	9	.87	58	35	1.13
L. compressa (Lea)	8	5	.50	10	6	.57	8	5	.49	26	16	.52
Subfamily Ambleminae												
Megalonaias nervosa (Rafinesque)	1	1	.10	1	1	.10	0	0	0	2	2	.06
Quadrula pustulosa (Lea)	0	0	0	0	0	0	1	1	.10	1	1	.03
Amblema plicata (Say)	2	2	.20	3	3	.29	2	1	.10	7	6	.19
Fusconaia ebena (Lea)	1	1	.10	0	0	0	1	1	.10	2	2	.06
F. flava (Rafinesque)	46	31	3.09	60	38	3.62	35	18	1.75	141	87	2.82
Elliptio crassidens crassidens (Lamarck)	0	0	0	0	0	0	1	1	.10	1	1	.03
E. dilatata (Rafinesque)	1246	643	64.04	1274	656	62.42	1372	712	69.13	3892	2011	65.19
Subfamily Lampsilinae												
Actinonaias ligamentina carinata (Barnes)	5	5	.50	3	2	.19	6	4	.39	14	11	.36
Potamilus alatus (Say)	2	1	.10	3	3	.29	5	3	.29	10	7	.23
Ligumia recta (Lamarck)	1	1	.10	0	0	0	0	0	0	1	1	.03
Venustaconcha ellipsiformis ellipsiformis (Conrad)	441	221	22.01	319	182	17.31	383	192	18.64	1143	595	19.30
Villosa iris iris (Lea)	0	0	0	1	1	.10	2	2	.19	3	3	.10
Lampsilis teres teres (Rafinesque)	0	0	0	0	0	0	2	2	.19	2	2	.06
L. teres anodontoides (Lea)	0	0	0	0	0	0	1	1	.10	1	1	.03
L. radiata luteola (Lamarck)	16	11	1.10	115	66	6.28	25	16	1.55	156	93	3.01
L. ventricosa (Barnes)	5	5	.50	25	14	1.33	11	6	.58	41	25	.81
Subtotals	1909	1004	100.02	1947	1051	100.02	1968	1030	100.01	5824	3085	99.98
Unidentifiable	17			24			9			50		
Totals	1926	1004	100.02	1971	1051	100.02	1977	1030	100.01	5874	3085	99.98

of certain subspecific designations for subfossil material in this report is in keeping with the catalogued voucher series at OSUM and serves to distinguish closely related taxa that differ in shell morphology and currently understood distribution, but are at present defined as distinct only at the subspecific level. The subspecific determination of *Anodonta grandis corpulenta* Cooper, 1834 for the modern Grant River material is based on identifications made at the OSUM. The subfossil *Anodonta grandis* from the Brogley and Preston Rockshelters deposited as vouchers at OSUM were assigned to *A. g. grandis* Say, 1829; however, valves are listed in this report as *A. grandis (sensu lato)* as the author lacked certainty in some subspecific identification.

SITE LOCATION AND DESCRIPTION

The Brogley Rockshelter is a prehistoric Indian site (state code number 47Gt156) located under a sandstone cliff adjacent to the Platte River in section 8, T3N, R2W, Grant

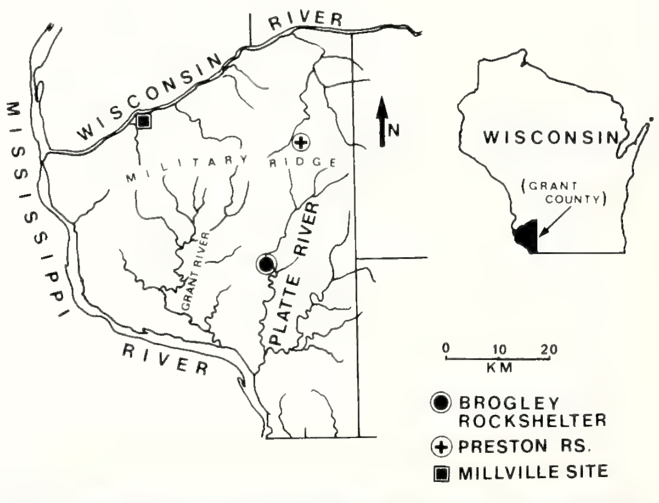

Fig. 1. Map showing location of Brogley Rockshelter, Preston Rockshelter and the Millville site.

County, Wisconsin (Fig. 1). This site was found to contain prehistoric Indian occupation refuse and sediment extending to a depth of 2.6 m below the surface when excavated by Mr. Robert H. Nelson between 1967 and 1971. Based on the recovered archaeological materials and radiocarbon dating, Brogley Rockshelter is divisible into two major periods of intermittent human occupation. The upper 1.5 m of the shelter deposit contained artifactual remains that indicate a Woodland cultural tradition occupation between A.D. 1 and A.D. 1200. The lower 1.1 m of the site deposit is an Archaic cultural component with artifacts and a series of radiocarbon determinations indicating most human occupation occurred between 2800 and 1 B.C. The radiocarbon dating and archaeological content of Brogley have been discussed by Bender *et al.* (1971), 1973), Emerson (1979), Geier and Loftus (1975) and Tiffany (1974).

PHYSICAL SETTING

The rough hill country of southwestern Wisconsin comprises much of the 35,000 km^2 Driftless Area (Martin, 1965; Roosa, 1984) with small portions extending into three adjacent states. This region lacks evidence for Pleistocene glaciation and is characterized by steep-sided, stony valleys dissecting the uplands with dendritic patterns of small stream development. The upland ridges and escarpments of the larger valleys exhibit 50 to 150 m of relief. The two prominent rivers crossing the region are the Mississippi, forming the western border of Wisconsin, and the Wisconsin River which drains a large area of central and southwestern Wisconsin. Both rivers were major meltwater channels during the terminal phases of the Pleistocene.

The southernmost county in Wisconsin, Grant, is bisected by an east-west trending drainage divide, the Military Ridge. To the north of this divide, streams drain into the Wisconsin River, and to the south into the Mississippi. One small river draining south is the Platte. In the vicinity of Brogley Rockshelter, the Platte River is 5 to 15 m in width with a series of riffles connecting pools. The drainage area of the Platte River above Brogley is approximately 365 km^2

Table 2. Freshwater mussel distribution by depth at Brogley Rockshelter.

Cultural Component:	Woodland				Archaic			
Approximate Date:	A.D. 1-1200				2800-1 B.C.			
Feet Below Surface:	0-0.4	0.4-1.4	1.4-2.4	2.4-3.4	3.4-4.4	4.4-5.4	5.4-6.4	6.4-7.4
Valve Side:	L/R	L/R	L/R	L/R	L/R	L/R	L/R	L/R
Family Unionidae								
Subfamily Anodontinae								
Anodonta grandis s.l.	—	0/1	3/0	2/0	3/0	3/8	—	—
Anodontoides ferussacianus	—	—	—	—	1/0	2/2	—	—
Strophitus undulatus undulatus	1/3	4/1	11/20	12/9	10/14	22/15	3/2	—
Alasmidonta marginata	4/2	7/2	8/6	4/3	2/5	10/4	2/0	
A. viridis	—	0/2	5/4	1/0	—	2/0	—	—
Arcidens confragosus	—	—	—	—	—	—	—	—
Lasmigona complanata	—	—	—	—	—	—	1/0	—
L. costata	2/2	2/0	5/6	1/2	4/2	11/3	1/1	—
L. compressa	—	1/1	2/2	0/2	2/2	2/3	0/1	—
Subfamily Ambleminae								
Megalonaias nervosa	—	—	—	0/1	—	—	1/0	—
Quadrula pustulosa	—	—	—	—	—	—	—	—
Amblema plicata	1/0	—	1/0	—	1/0	2/0	—	—
Fusconaia ebena	—	—	0/1	—	—	—	—	—
F. flava	3/1	8/0	17/9	3/5	9/12	27/10	2/0	—
Elliptio crassidens crassidens	—	—	—	—	—	—	—	—
E. dilatata	45/45	194/194	270/271	134/93	158/142	407/392	87/79	4/5
Subfamily Lampsilinae								
Actinonaias ligamentina carinata	—	—	0/3	0/2	0/1	1/0	—	1/0
Potamilus alatus	1/0	0/1	—	—	—	3/0	—	—
Ligumia recta	—	—	—	1/0	—	—	—	—
Venustaconcha ellipsiformis ellipsiformis	18/22	51/57	107/107	45/34	69/55	99/72	11/8	3/2
Villosa iris iris	—	—	—	—	1/0	—	—	—
Lampsilis teres teres	—	—	—	—	—	—	—	—
L. teres anodontoides	—	—	—	—	—	—	—	—
L. radiata luteola	—	2/0	1/1	8/4	16/9	45/36	4/3	1/1
L. ventricosa	—	1/0	1/0	1/2	5/2	2/11	3/1	1/0
Subtotals	150	529	861	369	525	1194	210	18
Unidentifiable Valves	2/0	1/2	0/2	7/3	5/3	8/2	5/1	0/0

(Holstrom, 1972) and this river enters the Mississippi River 16 km to the south of the site.

RESULTS

THE BROGLEY ROCKSHELTER MUSSEL ASSEMBLAGE

A total of 5874 freshwater mussel valves, representing at least 3085 individuals and 25 species were recovered through archaeological excavations at Brogley Rockshelter. The valves are grouped into the previously mentioned Woodland and Archaic cultural components identified for the site (Table 1) and by specific levels (Table 2). Approximately one-third of the total site assemblage came from unprovenienced contexts.

The most abundant mussel species recovered at Brogley was the spike, *Elliptio dilatata* (Rafinesque), representing 65.2% (= 2011 individuals) of the site total. With few exceptions, valves of *E. dilatata* from Brogley are the stream or small river ecoform [= *E. dilatatus delicatus* (Simpson) (see Baker, 1928)]. A small number of large, robust *E. dilatata* valves (n = 2 right, 4 left) seem to represent the large river phenotype characteristic of the Mississippi and lower Wisconsin rivers. In streams and small rivers *E. dilatata* can be found in moderate current on a sand and/or gravel substratum in 0.3 to 0.6 m of water (Baker, 1928). In eastern Wisconsin the author has found the small river ecoform of this taxon most densely concentrated on mixed silt, sand and gravel in quieter water at the margin of riffles and runs.

The ellipse mussel, *Venustaconcha ellipsiformis ellipsiformis* (Conrad), was second in abundance at Brogley with 595 individuals comprising 19.3% of the total assemblage. The ellipse is characteristic of streams and small rivers in eastern Wisconsin (Mathiak, 1979) and elsewhere in the Midwest (e.g. Van der Schalie and Van der Schalie, 1963; Parmalee, 1967; Oesch, 1984) where it is found on a substratum of sand and gravel in riffles and runs under a moderate to swift current (Baker, 1928; Van der Schalie and Van der Schalie, 1963). In the main stem Mississippi River the ellipse is a very rare extralimital species (Van der Schalie and Van der Schalie, 1950; Fuller, 1980a).

Elliptio dilatata and *Venustaconcha ellipsiformis ellipsiformis* together total 84.5% of the Brogley Rockshelter naiad assemblage with only five of the remaining 23 taxa contributing more than 1.0% each. These five are *Lampsilis radiata luteola* (Lamarck) with 93 individuals representing 3.0% of the assemblage; *Strophitus undulatus undulatus* (Say) with 2.9%; *Fusconaia flava* (Rafinesque) with 2.8%; *Alasmidonta marginata* Say, with 1.9% and *Lasmigona costata* (Rafinesque) with 35 individuals equalling 1.1% of the assemblage. The *F. flava* specimens are compressed headwater or small river ecoforms (see Ortmann, 1920). *S. u. undulatus, A. marginata* and *L. costata* are most abundant in small rivers and streams. Although *L. r. luteola* occurs in a wide range of aquatic habitats, the Brogley specimens represent a small river phenotype. Additional species at Brogley Rockshelter characteristic of small rivers and streams include *Alasmidonta viridis* (Rafinesque) with 17 individuals comprising 0.6% of the assemblage, *Lasmigona compressa* (Lea) with 0.5%, *Anodontoides ferussacianus* (Lea) with 0.1% and *Villosa iris iris* (Lea) with 3 individuals representing 0.1% of the Brogley naiades.

The remaining 14 naiad species at the site, each contributing less than 1.0% of the assemblage, are divided into two groups based on habitat association. The first group includes *Anodonta grandis, Lasmigona complanata* (Barnes), *Quadrula pustulosa* (Lea), *Amblema plicata* (Say), *Actinonaias ligamentina carinata* (Barnes), *Potamilus alatus* (Say), *Ligumia recta* (Lamarck), *Lampsilis teres teres* (Rafinesque), and *L. ventricosa* (Barnes). Taken together these nine species are represented by 71 individuals and comprise 2.3% of the assemblage. They can be found in a range of stream sizes from large to rather small rivers. It seems feasible that they were uncommon members of the prehistoric Platte River naiad community, although it is possible that some of these valves were brought to Brogley from sources other than the Platte River as raw material for tools or as curios. One of two *L. t. teres* valves has a humanly modified ventral margin indicating its use as a tool.

The second group of five species, each represented by one or two individuals at Brogley includes *Arcidens confragosus* (Say), *Megalonaias nervosa* (Rafinesque), *Fusconaia ebena* (Lea), *Elliptio crassidens crassidens* (Lamarck), and *Lampsilis teres anodontoides* (Lea). In southwestern Wisconsin these taxa seem associated with the large river habitats such as the Mississippi River or the lower Wisconsin River. Together, this group has seven individuals comprising 0.2% of the site assemblage. Many of the prehistoric peoples of southwestern Wisconsin were hunters and gatherers who moved on a seasonal round that included summer season harvest of freshwater mussels, fish and various other game along the Mississippi River. In the fall of the year these people often moved inland to winter hunting camps (Theler, 1983), such as Brogley Rockshelter. *E. c. crassidens* could have been brought to Brogley from the Mississippi River, its only known historic habitat in Wisconsin (Baker, 1928). The striking salmon colored nacre and large shell size could have contributed to the desirability of *E. c. crassidens* among prehistoric peoples. A valve of this taxon was found in association with a Woodland tradition human infant burial in the interior of the Driftless Area (Mead, 1979).

A possible source for valves of *Fusconaia ebena, Arcidens confragosus,* and *Lampsilis teres anodontoides* may be the Wisconsin or Mississippi rivers (Baker, 1928; Stern, 1983) but they would be unexpected or very rare in the Platte River. The *L. t. anodontoides* valve has a humanly modified ventral margin indicating its use as a tool. The river of origin for the two valves of *Megalonaias nervosa* is uncertain. This species exists in some numbers in the modern-day upper Mississippi River (Thiel, 1981; Duncan and Thiel, 1983), but was not present among the large assemblages of analyzed mussel valves from prehistoric Indian shell middens along the upper Mississippi River in southwestern Wisconsin (Theler, 1983). *M. nervosa* has been recovered as a rare species at prehistoric Indian sites along the Mississippi River in the Rock Island area of Illinois (Van Dyke *et al.*, 1980) and at La Crosse, Wisconsin (Stevenson, 1985). A single valve of *M. nervosa* was present at the prehistoric Millville archaeological site on the lower Wisconsin River (Theler, 1983) in Grant County, Wisconsin, but has not been recorded from that river in historic times (Baker, 1928; Mathiak, 1979; Stern, 1983). One of the two Brogley specimens is a large, heavy valve with a battered ventral margin indicating its use as a tool. Unfortunately, the more obvious artifacts fashioned from mussel shells presumably found at Brogley were not located during this study.

INTRASITE VARIABILITY

When compared to the Woodland component, the earlier Archaic occupation levels at Brogley Rockshelter contain a greater relative abundance of *Lampsilis radiata luteola, L. ventricosa, Anodonta grandis, Lasmigona costata* and the only provenienced *Anodontoides ferussacianus.* These taxa are generally associated with a low energy aquatic environment and a fine sediment substratum. The Woodland component contains a higher frequency of *Elliptio dilatata, Venustaconcha ellipsiformis ellipsiformis, Alasmidonta marginata,* and *A. viridis.* These last named species are most frequently associated with a moderate to strong current velocity over a substratum of sand and gravel. The component distribution may indicate greater availability or exploitation of low energy habitats with silt and/or sand substratum during the Archaic occupation at Brogley Rockshelter.

THE PRESENT-DAY PLATTE AND GRANT RIVERS

Today the Platte River is a stream with silt laden pools and it often carries a high load of suspended sediments. Nonetheless, it supports a substantial fish population (Fago, 1985) and contains many riffles and runs having a gravel/cobble substratum. Careful examination of several seemingly adequate habitats in the vicinity of Brogley in 1982 and 1985 failed to locate any living naiades or fresh shells. A few eroded valves of *Elliptio dilatata* were found mixed with the gravel/cobble substratum. It is possible that small, undiscovered naiad populations now exist in some portions of the Platte River.

Located immediately to the west of the Platte is the Grant River (Fig. 1), a stream similar to drainage configuration and size to the Platte. The Grant River contains a few small naiad populations; one location above the village of Burton contains living *Anodonta grandis corpulenta, Strophitus undulatus undulatus, Tritogonia verruscosa* (Rafinesque), *Quadrula quadrula* (Rafinesque), *Lasmigona complanata, L. costata* and *Lampsilis ventricosa.* Mussel valves from this locale that have been dead for an undetermined length of time included *Alasmidonta marginata, Fusconaia flava, Leptodea fragilis* (Rafinesque), *Potamilus alatus, Ligumia recta,* and *Lampsilis radiata luteola.* In a headwater branch of the Grant, the Little Grant River, living *Lasmigona costata* and *Lampsilis ventricosa* were found by the author in 1985. A single living *Venustachoncha ellipsiformis ellipsiformis* was also found in the Grant below Burton by David J. Heath in 1983.

INTERSITE COMPARISONS

At present, the prehistoric assemblage of freshwater mussel valves recovered at Brogley Rockshelter stands alone in its large sample size and species diversity for the smaller rivers and streams of the Driftless Area. An additional Driftless Area archaeological site in a small stream setting that has produced a series of mussel valves is Preston Rockshelter (47Gt157). This site is located on the north side of the Military Ridge adjacent to a tributary of Fennimore Creek, a branch of the Blue River that in turn empties into the Wisconsin River 19 km from the site in Grant County (Fig. 1). Excavations at Preston uncovered evidence for intermittent human occupation between 1000 B.C. and A.D. 1200. Although a large amount of humanly introduced animal bone (as food refuse) was recovered from the site, only 75 unmodified freshwater mussel valves of eight taxa were present (Theler, 1983).

The most abundant taxon in the Preston Rockshelter mussel assemblage was *Anodonta grandis* represented by 30 valves that comprise 40.0% of all shells recovered. Next in order of abundance were *Lampsilis radiata luteola* (14 valves, 18.7%), *Lampsilis ventricosa* (12 valves, 16.0%) and *Anodontoides ferussacianus* (10 valves, 13.3%). The remaining mussel species at Preston were *Potamilus alatus* (4 valves), *Elliptio dilatata* (3 valves), *Amblema plicata* (1 valve) and *Lasmigonia complanata* (1 valve), together totaling 11.9% of the assemblage.

The four most frequently occurring mussel species at Preston Rockshelter were taxa usually found living in low energy aquatic regimes. The abundance of riparian mammal bones (e.g. muskrat and beaver) and some waterfowl remains among the Preston bone refuse could indicate that headwater portions of Fennimore Creek were periodically impounded, perhaps by beaver dams, during the prehistoric occupation, thus enhancing the local habitat for certain mussel taxa such as *Anodonta* and *Anodontoides.* The four least common species at Preston Rockshelter may have been present in the Blue River or perhaps Fennimore Creek at some time in the past, although both streams appear devoid of living mussels today. The valves of *Elliptio dilatata* from Preston are the small stream ecoform.

The mussel assemblage from Preston Rockshelter is in sharp contrast to that found at Brogley where *Elliptio dilatata* and *Venustaconcha ellipsiformis ellipsiformis* together comprised the majority of recovered mussel valves and is interpreted as reflecting availability of suitable habitat for these species. The absence at Preston of *V. e. ellipsiformis, Alasmidonta viridis, Villosa iris iris* and the rarity of *E. dilatata* seems to indicate that the preferred habitat of these taxa, a small to medium sized stream having a stable gravel/sand substratum with a good current may not have been present in the vicinity of the site during its utilization.

Assemblages of freshwater mussel valves found at aboriginal sites adjacent to large rivers crossing the Driftless Area are distinct from those of small rivers in their species composition and phenotypic variation in shell morphology for certain taxa. On the lower Wisconsin River in Grant County (Fig. 1), the Millville site (47Gt53) was occupied by Woodland tradition peoples at about A.D. 400. Excavation at Millville in 1962 produced 174 mussel valves, with 20 species represented (Theler, 1983). The seven most abundant taxa were, *Fusconaia flava* with 25 valves representing 14.4% of the assemblage, *F. ebena* (20 valves, 11.5%), *Actinonaias ligamentina carinata* (19 valves, 10.9%), *Amblema plicata* (18 valves, 10.3%), *Elliptio dilatata* (15 valves, 8.6%), *Quadrula metanevra* (Rafinesque) (13 valves, 7.5%) and *Plethobasus cyphus* (Rafinesque) (10 valves, 5.7%). In southwestern Wisconsin, *F. ebena, Q. metanevra* and *P. cyphyus* are reported in the historic period only from the Wisconsin and Mississippi rivers (Baker, 1928; Mathiak, 1979; Stern, 1983).

A number of prehistoric mussel assemblages have been recovered at aboriginal sites along the main stem Mississippi River near the confluence of the Wisconsin and Mississippi rivers (Theler, 1983). In summarizing more than 29,000 mussel valves of 28 species recovered from seven Woodland tradition sites dating between A.D. 70 and A.D. 1200, *Fusconaia ebena* ranked first comprising 58.2% of the total, followed by *Quadrula metanevra* (7.7%), *Amblema plicata* (6.9%) and *Pleurobema sintoxia* (Rafinesque) (5.9%). *Elliptio dilatata* ranked ninth (1.5%) in relative abundance (Theler, 1987).

The assemblages from the Millville site and those along the main stem Mississippi River lacked many species typical of smaller rivers including *Anodontoides ferussacianus, Alasmidonta viridis, Lasmigona compressa, Venustaconcha ellipsiformis ellipsiformis* and *Villosa iris iris*.

Although no metric data have been collected, valves of *Fusconaia flava* from Millville and the seven Mississippi River sites are more inflated than the valves from Brogley Rockshelter, consistent with the magnitude of their apparent rivers of origin (see comments by Ortmann 1920:282-284, 310-312). The *Elliptio dilatata* are distinctly larger and heavier at sites located adjacent to the Wisconsin and Mississippi rivers when compared to the majority of specimens from Brogley and Preston Rockshelters, like *F. flava, E. dilatata* appear to exhibit strong phenotypic trends in shell morphology.

DISCUSSION

The prehistoric peoples who occupied Brogley Rockshelter could have introduced a few mussel valves into the site from sources other than the Platte River, possibly the main stem Mississippi River. The great majority of the Brogley valves appear to represent the remains of mussels gathered from the Platte River as a food source.

Taken together, most of the species at Brogley Rockshelter are typical of a small river naiad community with an assemblage composition similar to that found in modern-day streams of good water quality in eastern Wisconsin (Baker, 1928; Mathiak, 1979), but not in small rivers of Wisconsin's Driftless Area. The small river naiad community identified at Brogley became established in the Platte River some time before 4800 years ago. The most feasible route for arrival of naiad populations is through glochidia dropped from host fish that entered the Platte River drainage by way of the Mississippi River. The establishment of species extralimital to the main stem Mississippi (e.g. *Venustaconcha ellipsiformis ellipsiformis* and *Alasmidonta viridis*) would presumably be a rare event. Once established in Driftless Area small rivers, naiades could have experienced periodic population declines during episodes of severe flood erosion or siltation, with recovery during periods of low flood intensity. While the historic period is marked by the most intense Holocene erosion and sediment deposition (Knox, 1977; 1985), a few naiades survive as circumscribed populations in some Driftless Area streams. The single living *V. e. ellipsiformis* found in the Grant River is possibly a representative of a relict population surviving the regional habitat stress during the Twentieth Century.

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RESEARCH NOTE

SHELL MICROSTRUCTURAL RESPONSES OF *GEUKENSIA DEMISSA GRANOSISSIMA* (MOLLUSCA: BIVALVIA) TO CONTINUAL SUBMERGENCE

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In North America, the Atlantic ribbed mussel *Geukensia demissa* (Dillwyn, 1817) can be found intertidally in marshes from the Gulf of St. Lawrence to northeastern Florida (Abbott, 1974). There are two recognized subspecies of *G. demissa*, namely, *G. d. demissa* (Dillwyn, 1817) and *G. d. granosissima* (Sowerby, 1914) (Blackwell *et al.*, 1977). The latter is present along the Gulf Coast of Mississippi. Blackwell *et al.* (1977) suggested that the deposition of prisms found in the middle prismatic shell layer of the two subspecies was genetically regulated. Lutz and Rhoads (1978, 1980) and Lutz and Clark (1984) have shown seasonal and latitudinal variation in the inner shell layer of *G. demissa* inhabiting the Atlantic coast of North America. While juvenile *G. d. granosissima* are rarely found in subtidal habitats, adult ribbed mussels are never found subtidally (Heard, 1972). In this note, we report variation in growth of the internal shell nacre, induced by transplantation, of adult *G. d. granosissima* to a continuously submerged habitat in Ocean Springs, Mississippi.

Field experiments were carried out twice, a preliminary study in 1984 (3 March to 31 March) and a final study in 1985 (19 January to 23 February). Live mussels collected from emerged salt marsh (substratum normally exposed to air 50% of the time) fronting the Gulf Coast Research Laboratory, Ocean Springs, Mississippi, were divided into three groups of 20 mussels each. One group was shucked immediately and acted as a baseline for "normal" shell microstructure. Each of the other two groups was subdivided and placed into two separate wire mesh cages. One set (2 cages of 10 mussels each) was returned to the original site of collection [this habitat (emerged) was exposed to air during initial and final collection of mussels]. The other set was transplanted to a submerged area (substratum never exposed to air) less than 50 m seaward of the original collection site. Both sets of cages were set out within seven hours after initial collection. After about one month, shell microstructure of the caged mussels was examined by scanning electron microscopy and compared with baseline samples.

Adjusted 1985 tides for Biloxi Bay, Mississippi, indicated a tidal range from −27 cm to +58 cm. Predicted tides for 19 January 1985 were −27 cm (0750 hr) and 58 cm (2108 hr). Predicted tides for 23 February 1985 were 30 cm (0119 hr), 9 cm (0807 hr), 27 cm (1300 hr) and 6 cm (2054 hr).

A warming trend in air and water (19.0-25.0°C) occurred during the 1985 experiment (including freezing and temperatures from 20 to 23 January 1985). Salinity in Mississippi Sound varies from 0 to 16 ppt (Hackney and Cruz, 1982) and is usually low in winter and highest in March. Values we obtained correspond to reported values. Differences in the internal shell surface microstructures point to differences between regularly emerged and continually submerged habitats.

Areas of internal shell surface examined microstructurally are shown in plate 1. Based on 12 baseline mussels examined in January 1985, the internal shell surface of *Geukensia demissa granosissima* from Ocean Springs basically consists of the following shell microstructures: Starting from inside the pallial line, the "typical" nacre (Plate 1, Fig. A) composing the area towards the center of the shell (Plate 1, I_2) can be eroded to the extent that it appears homogeneous. This nacreous zone is adjacent to an area (Plate 1, I_2) composed of homogeneous [*sensu strictu (s.s.)*] microstructure whose granule sizes and shapes are less regular than those of the homogeneous (*s.s.*) microstructure in submerged mussels (Plate 1, Fig. B). A narrow transition zone leads to the pallial line composed of myostracum. This pallial myostracum (Plate 1, P) consists of short prisms (Plate 1, Fig. C) while the adductor scars (Plate 1, A) consist of tall prisms (Plate 1, Fig. D). Outside the pallial line, nacre (Plate 1,

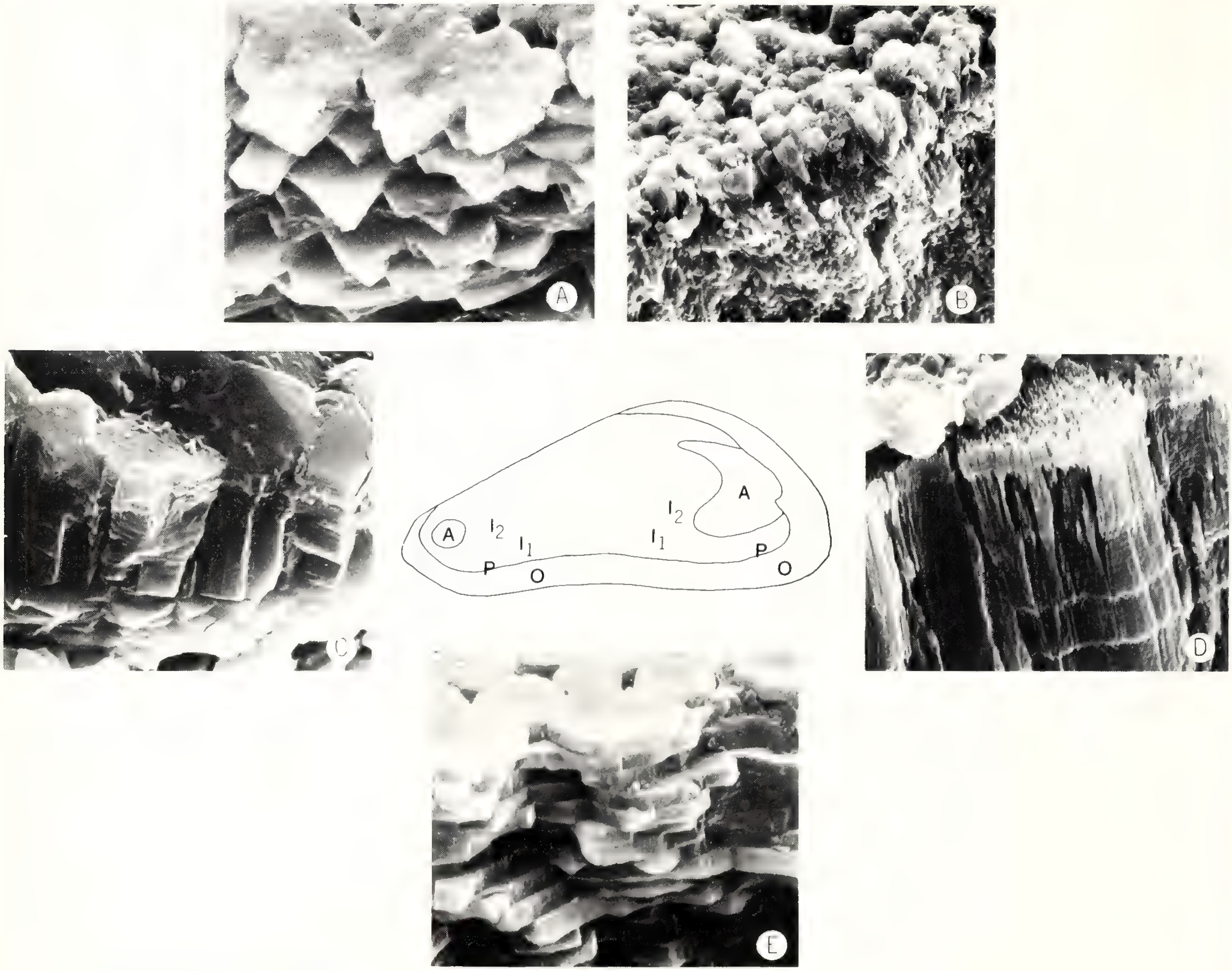

Plate 1. Central line figure represents right valve of *Geukensia demissa granosissima* (internal shell surface with retractor scars omitted) surrounded by micrographs of corresponding shell microstructure (45^0 angle view of fractures with internal shell surfaces towards the top). Horizontal field width of micrographs = 16 μm. **A.** Nacre towards shell center (I_2). **B.** Homogeneous (*s.s.*) just inside pallial line (I_1). **C.** Short prisms composing pallial line (P). **D.** Tall prisms of adductor myostracum (A). **E.** Nacre between pallial line and outermost rim of shell (0).

Fig. E) again makes up the internal shell surface. The internal shell surface microstructure of the outermost rim (i.e. peripheral edge), however, can also be prismatic, blocky prismatic or homogeneous (*s.s.*). Variation of internal shell surface microstructure in the outermost rim can be a reflectoin of intermediate steps in the production of typically multiphasic outer shell layers.

We predicted that baseline and experimental emerged mussels would have similar internal shell microstructure unless the emerged mussels were "impinged" by the environment (over the one month duration of the experiment) or influenced by a cage effect. Indeed, these two groups were similar in internal shell structure with minor exceptions. Emerged mussels lacked the well formed nacre (mature tablets and growing nuclei) that were found in isolated pockets inside and outside the pallial line of baseline mussels.

For the comparative study of internal shell surface microstructures of emerged verus submerged mussels, only mussels of similar lengths (about 50 mm) were used. The main difference between emerged and submerged mussels in 1984 (limited sample) was in the posterior region of the shell outside the pallial line (Plate 2, Figs. A-B). Sizes and shapes of tablets in submerged mussels (Plate 2, Fig. A) were different from those of emerged mussels (Plate 2, Fig. B). Tablets of the former were elongated along one axis.

The 1985 transplantation experiment yielded greater internal shell surface microstructural differences between emerged and submerged mussels (Table 1). Relevant results presented in table 1 were based on examination of 10 valves of 10 individuals for each of the emerged and submerged mussels.

Some emerged mussels had elevated borders of continuous ridges, beads (Plate 2, Fig. C) or granules that partially or completely surrounded one or more tablets along their 001 faces. These circumferential ridges resemble those structures attributed to shell formation and growth in *Pinctada martensii* (Dunker) (Wada, 1960, 1961), ring nacre of *Mytilimeria nuttalli* Conrad and *Lyonsia californica* Conrad (Prezant, 1981) and those attributed to shell dissolution in *Geukensia demissa* (Wilkes and Crenshaw, 1979; Rhoads and Lutz, 1980). Emerged mussels that exhibited these shell microstructures have fragmented and pitted tablets predominating in their internal shell surface (Table 1). The predominance of erosive remnants of nacre, both inside and outside the pallial line of emerged mussels (Table 1), indicates shell dissolution. Contrary to expectations, the warming trend in the weather inhibited shell formation in emerged mussels (absence of crystal nuclei, growing tablets and smooth surfaced tablets, etc.). Possibly a short cold spell following the day mussels were transplanted could have increased stress associated with the emerged habitat. One could speculate that the circumferential beads (Plate 2, Fig. C) are anlages to mature microstructures if one assumes that the emerged mussels were at a stage of recovery from shell dissolution (shell formation being initiated in response to changing

Table 1. Internal shell surface microstructures of *Geukensia demissa granosissima* after field experiment (1985) (– = absent, + to + + + + = degree of presence of microstructure in internal shell, where + = 1-25%, + + = 26-50%, + + + = 51-75%, + + + + = 76-100%).

	Emerged Mussels	Submerged Mussels
A. OUTSIDE THE PALLIAL LINE		
1. anterior region		
—crystal nuclei and growing tablets	–	+
—smooth surface tablets	–	+
—pitted tablets	+ + + +	+
—ridged, beaded and granulated tablets	+	–
2. posterior region		
—crystal nuclei and growing tablets	–	+
—smooth surface tablets	–	+
—pitted tablets	+ + + +	+
—ridged, beaded and granulated tablets	–	–
B. INSIDE THE PALLIAL LINE		
1. anterior region		
—erosive remnants of nacre	+ + + +	+ +
—homogeneous (granules shape and size)	variable	uniform
2. posterior region		
—erosive remnants of nacre	+ + + +	+ +
—homogeneous (granules shape and size)	variable	uniform

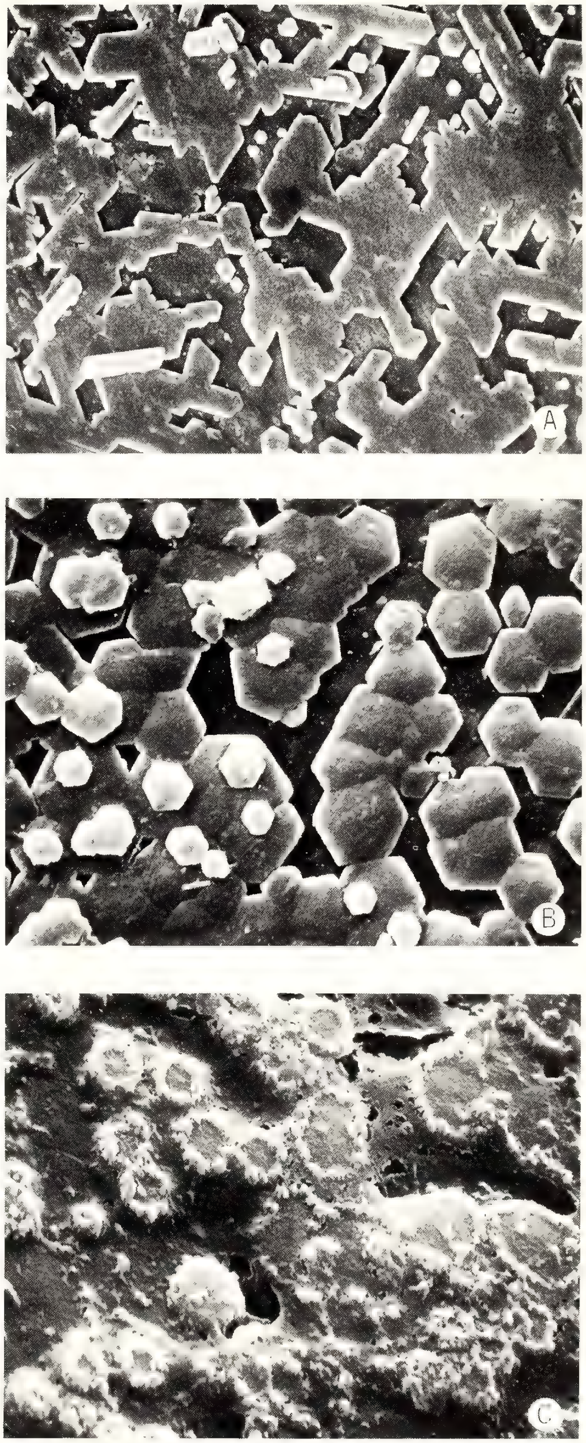

Plate 2. A. Internal shell surface consists of elongated solitary and fusing polygonal tablets (Posterior region of submerged mussels, area O, March 1984). Horizontal field width = 22.8 μm. **B.** Internal shell surface consists of typical hexagonal tablet in various states of fusion (Posterior region of emerged mussels, area O, March 1984). Horizontal field width = 22.8 μm. **C.** Internal shell surface consists of peripherally beaded tablets (Anterior region of emerged mussel, area O, February 1985). Horizontal field width = 22.8 μm.

stressful to a more favorable condition). However, based on the overall picture and the presence of irregular pittings on the organic matrices where these structures were observed, we conclude that they are the result of incomplete dissolution.

Homogeneous (*s.s.*) internal shell surface microstructures in emerged mussels consisted of variably shaped granules, while those of submerged mussels consisted of uniformly shaped granules (Plate 1, Fig. B).

The uniformity of granule size and shape of homogeneous microstructure in the submerged mussels could be the result of well regulated formation. The assumption that shell formation is occurring in the submerged mussels is also supported by the presence of crystal nuclei and smooth surfaced tablets (Table 1) and apparent organic formations between and over tablets.

Mussels used in this experiment were taken from the same place at the same time. This assumes similarity of previous environmental influence at the start of the experiment. Furthermore, since the mussels utilized in this study were of similar size, variability due to age differences should be negligible. Growth rate of *Geukensia demissa* is higher along the marsh edge than in the higher marsh (Bertness and Grosholz, 1985). This, together with our observations, led us to hypothesize here that the submerged habitat is more stable, if not throughout the lifetime of the mussels, at least in this experiment. The surrounding water presumably acted as a buffer against severe weather variation. Continuous presence of water also insured access to food and nutrients and ready elimination of unwanted metabolic by-products. Normally, adult marsh mussels never occur subtidally; perhaps this is a reflection of blue crab or other predatory activities upon juvenile mussels (Bertness and Grosholz, 1985). In our experiments submerged mussels were protected from predators by cages. Continuous submergence of these protected mussels stimulated shell deposition and minimized shell dissolution.

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RESEARCH NOTE

EFFECTS OF CURRENT VELOCITY ON THE FRESHWATER BIVALVE *FUSCONAIA EBENA*

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ABSTRACT

As part of a research program on environmental effects of commercial navigation traffic, juvenile *Fusconaia ebena* (Lea) were exposed to three water velocity treatments in the laboratory. Changes in respiration rates and tissue condition were measured. Different experimental conditions were created by manipulating magnitude and duration of water velocities. Water flowed over gravel in which the mussels were positioned. The three treatments were: continuous-low (7 cm/s), continuous-high (27 cm/s), and cyclic-high water velocity which consisted of 5 min of high followed by 55 min of low velocity flow per hour. Tissue condition index (TCI, the ratio of tissue to shell dry mass) of *F. ebena* exposed to continuous-high turbulence was significantly less (0.05 level, Duncan's multiple range test) than TCI of mussels exposed to continuous-low or cyclic-high velocity. TCI of mussels in the latter two treatments did not significantly differ. There were no significant postimpact differences among respiration rates of mussels in the three treatments.

The passage of a commercial vessel through a waterway causes a brief change in water velocity that is usually accompanied by rapid drawdown and surge. Wuebben *et al.* (1984) reported a three-fold increase in bottom velocity and a 360° rotation in current direction immediately following commercial vessel passage in the St. Mary's River, Michigan, U. S. A. Eckblad (1981) determined that downbound tows in the upper Mississippi River caused current velocity to double. Concern has been expressed (e.g. Rasmussen, 1983) that this disruption in flow could negatively affect growth and survival of freshwater mussels (Unionaceae), a resource with commercial and ecological value. Typically, mussels inhabit channel border areas rather than main navigation channels (Coker *et al.*, 1921); however, physical effects of commercial traffic, while more severe in main channels, also take place in adjacent shallow water.

This note reports results of a laboratory study of the effects of exposure to continuous and cyclic periods of high water velocity on respiration and tissue condition of juvenile *Fusconaia ebena* (Lea), a thick-shelled unionid common in the lower Ohio River (Miller *et al.*, 1986).

METHODS

Seventy-two juvenile *Fusconaia ebena*, ranging in shell length from 17 to 26 mm were collected at Ohio River Mile 967, near Olmsted, Illinois, on 27 Aug 1985. The mussels were in a distinct mussel bed that supported a dense and diverse molluscan community (Miller *et al.*, 1986). Water depth where mussels were collected ranged from 3 to 5 m. River stage was near the average annual minimum at time of collection. Mussels were brought to the laboratory in Vicksburg, Mississippi, and gradually acclimated to aged dechlorinated tap water.

On 9 Sept, the 72 mussels were divided into three groups of approximately equal size distribution. Each group was exposed to one of three conditions: continuous-low, continuous-high, and cyclic-high water velocity. The experiment was conducted in three identical 200 *l* plexiglas chambers connected by a central mixing reservoir. The three conditions were created by manipulating the magnitude and duration of velocities of water flowing over gravel in which mussels were positioned (Table 1). Low-velocity flow (7 cm/s)

Table 1. Means and standard deviations of water velocity exposure, tissue condition index, and respiration rate measurements of juvenile *Fusconaia ebena* in three velocity exposure treatments. Mussels in the cyclic-high treatment were exposed to 5 minutes of high followed by 55 minutes of low velocity flow per hour. (Superscript letters a and b indicate which means were not significantly different at the 0.05 level using Duncan's Multiple Range Test; TDM, tissue dry mass; SDM, shell dry mass; percent reduction is relative to the tissue condition index of juvenile *F. ebena* fixed in the field upon collection on 27 August.)

	Velocity Exposure Treatment		
Variable	Continuous Low	Cyclic High	Continuous High
Water velocity (cm/s)			
Low	7.11 ± 1.02^a	6.60 ± 1.02^a	
High		26.42 ± 1.27^a	27.18 ± 3.56^a
Tissue Condition Index			
(TDM/SDM) x 100	1.72 ± 0.19^a	1.69 ± 0.30^a	1.43 ± 0.27^b
Percent Reduction	19.73 ± 8.39^a	22.39 ± 13.84^a	34.48 ± 12.50^b
Respiration Rate			
μmoles 02 / (mg x hr)	1.45 ± 0.27^a	1.46 ± 0.55^a	1.75 ± 0.58^a

was created by continuous operation of a small centrifugal water pump submersed in each tank. A larger pump ran continuously in the continuous-high velocity treatment, creating a 27 cm/s flow. In the cyclic-high velocity treatment, the larger pump was activated for 5 min each hour with a programmable electronic timer. Water was maintained at 22 ± 5°C and contained an *ad libitum* but nonfouling suspension of brewer's yeast for the duration of the 37 day experiment. Nutritionally adequate feeding of filter-feeding bivalves in a small, closed system is difficult. The yeast suspension was provided for simplicity and because previous unpublished studies in our laboratory have shown that the yeast cells are ingested and used in partial support of maintenance metabolism.

On days 33, 35, and 37 eight mussels were removed from each of the three treatments to measure respiration and tissue condition. Respiration was measured by incubating each mussel in a 300 ml jar of water overnight in the dark at 22 ± 0.5°C. After incubation, a 60 ml aliquot was siphoned from each jar, and dissolved oxygen determinations were made on each aliquot by Winkler titration. Three blanks were tested with each batch to determine bacterial oxygen uptake. Following determination of respiration, soft tissue was removed from the shell, and all tissues and shells were dried for 48 hr at 65°C and separately weighed. A tissue condition index (TCI) was obtained by dividing tissue dry mass (TDM) by shell dry mass (SDM) (both in mg) and multiplying the quotient by 100. A batch of juveniles fixed in 12% neutral formalin upon collection of 27 August was treated in an identical manner to estimate initial TCI.

RESULTS AND DISCUSSION

The TCI of juvenile *Fusconaia ebena* in the continuous-low and cyclic-high velocity treatments was 20% and 22% less than the TCI of field-fixed juveniles. Continuous exposure to conditions in the high velocity water test tank caused a 34% reduction in TCI. Comparison of the mean TCI by Duncan's multiple range test indicated that weight loss was not significantly different ($p < 0.05$) between continuous-low and cyclic-high velocity treatments, but weight loss was significantly less in these two treatments than in the continuous-high velocity group (Table 1). Respiration rates, measured in still water, did not differ significantly among mussels from the three treatments.

Sustained changes in hydrologic conditions were known to affect pumping and filtration rates of marine lamellibranchs. These molluscs are sensitive to changes in flow (Kirby-Smith, 1972; Walne, 1972) and to small differences in pressure between the inhalent and exhalent siphons (Hildreth, 1976). In addition, differences in the shape of unionids can be attributed to hydrologic conditions (Van der Schalie, 1941; Clarke, 1982; and references cited therein). With respect to turbulence, Brown *et al.* (1938) observed that the degree of stunted growth in unionids from the western basin of Lake Erie was positively correlated to the extent of exposure to waves.

The present experiment demonstrated that juvenile *Fusconaia ebena* are not residually affected by 5 min exposure to high velocity flow once per hour in postimpact measurements. Commercial traffic rates in the upper Mississippi River and Ohio River do not often exceed one tow per hour (personal observations). Thus, turbulence caused by routine traffic is not likely to deleteriously affect mussels. Conversely, at sites where barges are fleeted, towboats sometimes work essentially continuously (personal observations). Potential impacts to mussels by abrupt water velocity changes in fleeting areas need to be evaluated on a site-specific basis.

Discharge of the lower Ohio River varies widely on a seasonal basis such that the range of water velocities experienced by mussels in the field is greater than the range between low and high flows used in the laboratory study. Parmalee (1967) reported that *Fusconaia ebena* inhabits sites with "swift current," although the population providing animals for the present experiment thrives in a slight current during normal summer and fall flows (Miller *et al.,* 1986).

The extent to which *F. ebena* is representative of growth and physiology of other unionids in large rivers has not been investigated. However, previous workers (Parmalee, 1967; Fuller, 1977; Buchanan, 1980) indicate that *F. ebena* was, and in many cases still is (Miller *et al.*, 1986), a major component of gravel bar communities in large waterways.

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SYMPOSIUM ON THE BIOLOGY AND EVOLUTION OF OPISTHOBRANCH MOLLUSCS

ORGANIZED BY
TERRENCE M. GOSLINER
and
MICHAEL T. GHISELIN
CALIFORNIA ACADEMY OF SCIENCES

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MONTEREY, CALIFORNIA
2 - 3 JULY 1986

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My introduction to molluscs was through my husband, Ernst Marcus. Ernst was born in 1893 in Berlin. His family lived near the Berlin Zoo. During his school years, he passed almost all his free time watching the animals there. Ernst studied zoology at the University of Berlin until the beginning of World War I in 1914. He then joined the Cavalry where he received the First Class Iron Cross, an honor in Germany. After the war, in 1919, he received his Ph.D. with a thesis on the Coleoptera. After college, Ernst went to study at the Berlin Museum where he was assigned the phylum Bryozoa. He was Privatdozent (lecturer) in 1923 and Research Assistant of the Institute of Zoology by November 1923. He received the title of Professor in 1929.

I was born in Berlin in 1901. I am both the daughter and granddaughter of university professors of physiology. At ten years of age I obtained the microscope my father acquired in 1885. My first experience was to examine a dish of lake water and investigate its fauna: *Daphnia* and the like. After the ten-years-Lyzeum (primary and secondary school), 1908 to 1917, I took two courses in laboratory techniques and got a job at a university hospital in Bonn. While there, I was sent to Ernst Leitz-Wetzlar to learn microphotography. At the hospital I met Professor Wilhelm Schmidt (Bonn), and during my free Saturday afternoons I made many microphotographs for his book on polarisation. During my next vacation I enrolled in his course in living marine invertebrates. There I met a pharmacologist, Dr. Handovsky from Gottingen. Having worked for two years at the hospital in Bonn, 1920-21, I went to work with him during 1922.

Following my employment at the hospital, my father sent me to the Zoological Institute of the University of Berlin where I took two semesters of invertebrate zoology. During the second semester I met Ernst Marcus. We became engaged very soon and were married in March 1924. Being descended from the artist Daniel Chodowiecki, I was very good at scientific drawing. Consequently, I did all the illustrations for Ernst's publications. Ernst was multi-talented. He published on systematics, anatomy, embryology, physiology, zoogeography, and evolution. During the early years, from 1919 onward, he studied the Bryozoa. Later in 1927 he also studied the Tardigrada, freshwater Bryozoa, Malacopoda, mechanics of development of vertebrates, Protozoa, Hydrozoa, Pycnogonida, Oligochaeta, Nemertina, Turbellaria, Archiannelida, Opisthobranchia, and a few prosobranch groups. Before we were married, Ernst authored the first 20 papers of our list of about 220 publications. From 1925 on, I sometimes appeared as the sole author and later as coauthor. Since 1970, I have published some 30 papers alone, all on Opisthobranchia.

When Hitler gained power in 1933, the Jews were dismissed from their jobs except for those that Hindenburg protected because of their status, being heroes awarded the First Class Iron Cross. After Hindenburg's death, even the heroes were dismissed. We were spared as Ernst had received a Professorship at the New University of São Paulo, Brazil, in 1936. Although unaware at the time, this good fortune was due to the help of an English organization, headed by Lord Beveridge, to help the dismissed Jews. We did not learn of his sponsorship until 25 years later when Lord Beveridge asked Ernst how he was getting along.

In 1963 Ernst retired at 70 years old. Five years later he passed away. Since then I have been living along, going to the Zoology Department of the University of São Paulo regularly. In 1976, I received an honorary doctorial degree from the University. In 1985, I was told that the University of Aix-Marseille was preparing the same honorarian for me, but until now I have not received it.

ON SCIENTIFIC NAMES

Ernst and I are responsible for describing many new species and new genera. When naming new species, we tried to avoid using descriptive words describing morphological characters, i.e. *tridecemlineatus*. The Rules of Scientific Nomenclature allow for nonsense words and so sometimes we used any word that sounded good or that we liked. We had a long list of names found on occasions. *Dondice* was a name of a firm in São Paulo, Brazil. After we had published it, they changed their name to Dondicci. We would not have chosen that one. *Hallaxa apefae* was named for Alice Pruvot Fol, *A.P.F. Anisodoris prea* got the name of the Brazilian guineapig. *Plocamopherus gulo* was named after the greedy wolverine *Gulo. Miesea* was taken from Miese, a German name for cat. *Eubranchus coniclus* was derived from the name of rabbits. *Catriona maua* again was named after a cat. *Piseinotecus* is an entire sentence in Portuguese. Our friend, Diva, stated it while coming down the stairs one day. She had stepped upon our dog, Teco, and while we were looking for a new generic name, had told us Pisei (in Portuguese) = I stepped; no = onto; Tecus = the dog's name. In the meantime, this genus has turned out to be the type of a new family. Piseinotecidae appears in the literature today. There are many, more or less funny, names we have given species but I think these examples are sufficient.

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[1] The following autobiographical sketch was written and presented by Eveline du Bois-Reymond Marcus on the occasion of the Biology of Opisthobranchs Symposium held in her honor at the July 1986 American Malacological Union meeting in Monterey, California, U.S.A. The edited manuscript, essentially derived from her written opening remarks for the Symposium, sets the historical tone for this important series of opisthobranch papers. —*Editor*

LOOKING BACK

On Saturdays and Sundays Ernst and I always took a long walk for pleasure and for exercise. I do so still, going to the post office to pick up my mail. On weekdays my neighbor takes me to the Department at seven in the morning and brings me back for lunch, which his wife prepares. They both do everything possible for me. They treat me as if I was their mother.

Since 1968 I have made a two to four month trip to the United States and Europe at least every two years to see colleagues. I have also made trips to South Africa and Israel.

I am happy to say I do not have any health problems, but I do feel that my memory is failing. I am afraid that soon I will have to begin a paper as the Danish Opisthobranchologist Rudolf Bergh did in 1908: This is, in my 84th year, my last publication.

COLOR IN OPISTHOBRANCHS

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ABSTRACT

Evidence for the possible functions of color in opisthobranchs is reviewed. There is no evidence for the occurrence of intraspecific color signals, nor for fortuitous colors, so it is probable that all colors function in interspecific contexts, most (or perhaps all) being anti-predatory in function.

There is abundant evidence for crypsis in opisthobranchs and from this certain nudibranchs have evolved precise 'special resemblances' to their food in the form of sponge or coelenterate mimicry. Some can change color to match their food by sequestering pigments from it.

Warning colors and müllerian mimicry probably occur in some opisthobranchs, but evidence for these functions is largely indirect. Colors can also be used in a few species to deceive predators (flash coloration); to intimidate them (deimatic behaviour); or to direct attacks to expendible and/or noxious parts of the body (deflective marks), but experimental studies are lacking. There is tremendous scope for critical experimental studies of color in predator-prey interactions in opisthobranchs.

Typical gastropods have a coiled shell into which the body can be withdrawn when the animal is attacked by a predator. Many predators, however, have evolved ways of overcoming the defensive shell of gastropods, and as a consequence many gastropods have evolved additional anti-predator defensive adaptations, most notably chemical defences (Ansell, 1969; Edmunds, 1974). These chemical defences must have been a preadaptation for the evolution of opisthobranch molluscs which have reduced or even completely lost the shell. In a mollusc that was well protected by means other than the shell, the shell would have been a positive liability for several reasons: it is heavy; it provides anchorage for tube feet of starfish; its formation requires considerable expenditure of energy; it restricts the available position in the body for the gills and for the anal, renal and reproductive openings; it has a characteristic outline that is difficult to conceal; and it constrains the possible evolution of different body shapes and habits. It is no doubt for these reasons that the shell has been reduced and lost independently in the Nudibranchia, Ascoglossa (= Sacoglossa), Aplysiacea and Bullacea. These naked molluscs or sea-slugs have the entire dorsal surface available for the anal, renal and reproductive openings and for gaseous exchange (instead of these being confined to the mantle cavity or lateral mantle groove), and it can also be fashioned into a variety of shapes with firm or flexible processes such that the characteristic outline of the animal is totally obscured. Such processes can be used for respiration, defence, or digestion (by containing within them extensions of the gut). The mantle and its processes can also be protectively colored, and it has long been recognised that protective coloration is widespread in opisthobranchs (Garstang, 1890). Protective coloration in the context of the varied defensive adaptations of nudibranch molluscs has been reviewed by Edmunds (1966a, 1968a, 1974), Harris (1973), Ros (1974, 1976, 1977), Thompson (1976) and Todd (1981). Color, however, can have functions other than protection, and it is necessary to review these possible functions of color in opisthobranchs before assuming that all coloration is necessarily protective.

THE FUNCTIONS OF COLOR IN ANIMALS

The functions of external colors of animals can be considered in three categories:

1. INTERSPECIFIC SIGNALS. Color marks in animals can act as releasers of behavior in other species. Such behavior can be mutualistic as with the cleaner fish whose color signals are recognised by 'customer' fish (Edmunds, 1974), but more usually they function in a defensive context. Aposematic colors warn a predator that an animal is distasteful, and deimatic colors startle a predator (Edmunds, 1974). Cryptic colors by contrast emit signals that are indistinguishable from background noise. They function to reduce the chances of a predator finding an animal. Following Robinson (1969) and Kruuk (1964), Edmunds (1974) distinguished primary

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defences, which operate before a predator initiates prey-catching behavior, from secondary defences, which operate when an animal encounters a predator. Primary defences which involve coloration are crypsis, aposematism and batesian mimicry, and secondary defences are flight (flash behavior), deimatic behavior and deflection of an attack (Edmunds, 1974). In this paper these six headings will also be used in examining the defensive behavior of opisthobranchs, but one further heading has been added: special resemblance. Batesian mimics typically resemble active, aposematic animals, but there are also mimics of sessile objects including sticks, leaves and bird-droppings. Edmunds (1974) included these in batesian mimicry, but Vane-Wright (1980, 1981) prefers to regard them as crypsis. This is of relevance in opisthobranchs because some species appear to have very precise resemblances to sponges and coelenterates. The distinction between crypsis and mimicry is discussed by Cloudsley-Thompson (1981), Edmunds (1981a), Endler (1981), Robinson (1981), Rothschild (1981) and Vane-Wright (1981), but here I have evaded the problem by following Cott (1940) and classifying extreme forms of crypsis which resemble specific sessile animals as 'special resemblance'.

2. INTRASPECIFIC SIGNALS. Colors and certain specific behaviors can also act as signals which release a particular behavior in another individual of the same species. Examples are courtship and territorial behavior in many birds and fish such as the stickleback (*Gasterosteus aculeatus* L.), and pecking by herring gull chicks (*Larus argentatus* Pontopidan) at the red spot on the beak of its parent (Tinbergen, 1951). A more unusual example is the dummy eggs on the anal fin of male *Haplochromis burtoni* Günther which stimulate the female to attempt to snap these up into her mouth along with the real eggs. In doing this she engulfs sperm which fertilise her eggs (Wickler, 1968). Signals such as these can only function in animals that have good eyesight.

3. FORTUITOUS COLORS. The colors could be the result of selection pressures quite unrelated to the visual system of any observers of either the same or different species. The pigment deposited in the skin would be the outcome of some biochemical process whose importance was unrelated to the color it produced. Such coloration could be non-adaptive and could actually be to the animal's disadvantage if it is outweighed by the advantage of the associated biochemical process.

This is a difficult hypothesis to prove, but it is possible to test for its occurrence in permanently dark environments where colors cannot possibly have any intra- or inter-specific function. If fortuitous colors occur in these environments we can make two alternative predictions:

1. Each species would evolve a unique coloration either because it retained the adaptive colors of its ancestors from light environments, or because its genes for some specific biochemical process are linked to body color;
2. A group of unrelated species would convergently evolve a particular color because this color is the outcome of some biochemical process of adaptive importance in that environment.

However, if fortuitous colors do not occur then one could predict that in a totally dark environment there would be selective advantage to animals conserving energy by not manufacturing pigment; such white animals would have more energy available for reproduction and could, in the course of time, outreproduce pigmented individuals.

These predictions can be tested in three areas: in the deep sea, in underground caves, and deep in soil, sand or mud. In the deep sea, where there is no or very little light, many animals are red or black (Hardy, 1956). The evidence, however, indicates that in crustaceans and fish these colors are not fortuitous but are adaptations that make the animals cryptic in the dim light descending from above or produced by luminescent animals. In the hadal region where there is no trace of sunlight many fish have reduced eyes but are still pigmented black. This pigment is probably of protective value because there are some fish with luminescent 'searchlight' organs and exceptionally large eyes which would find unpigmented fish more easily (Marshall, 1979). Gastropods from deep sea trenches, however, are often white and lack eyes, so presumably there is no protective advantage for them to have pigment.

In underground caves, there is also perpetual darkness, but animals here totally lack body pigment so are either whitish or transparent. These animals have evolved from normally pigmented ancestors that entered the caves.

In animals that burrow deeply in soil, mud or sand and never come to the surface there would be no advantage in terms of camouflage in having dorsal skin pigment, so we might expect fortuitous colors to occur. *Collembola* living near the soil surface are typically dark brown or grey and so are well camouflaged whenever they are fully exposed, but species that live deeper where there is no trace of light are white and entirely lacking in pigment (Kühnelt, 1961). The available evidence, therefore, does not support the occurrence of fortuitous colors in the deep sea, in caves or in soil and sand, but no critical examination of evidence for fortuitous colors in opisthobranchs has been undertaken.

INTERSPECIFIC SIGNALS

CRYPTIC COLORATION - CAMOUFLAGE

There is a large literature of reports of opisthobranchs being cryptic on their normal background. Very often the normal background is actually their food, as with dorids which feed and rest on sponges. Ros (1976) and Todd (1981) recognise various categories of crypsis based on Cott (1940) and earlier workers, for example homochromy (resemblance of color), homotypy (resemblance of body form), disruptive coloration, countershading and elimination of lateral shadow. Most cryptic opisthobranchs exhibit more than one of these adaptations, but there is practically no evidence to show that any apparently cryptic opisthobranch is less likely to be found and eaten by a predator when camouflaged on its normal background than when relatively conspicuous elsewhere. Cryptic coloration will evolve only if there is selective advantage accruing to cryptic individuals in terms of reduced detection and killing by predators. Nevertheless, in the absence of such evidence, if we can show that there are elaborate adaptations which improve crypsis to human eyes, then it is reasonable to assume that these adaptations have evolved through predator selection. The survival value of camouflage has been demonstrated many times in other animals such as grasshoppers, mantids and fish (Cott, 1940; Edmunds, 1974).

The dorids *Archidoris pseudoargus* (Rapp) from Europe and *A. montereyensis* (Cooper) from California are mottled yellowish brown and cryptic on their normal food the sponge *Halichondria panicea* (Pallas). The spicular mantle has a similar texture to the sponge so that even when not resting on their food these dorids still resemble sponges. Red dorids of the genus *Rostanga* are similarly found on red sponges, *R. rubra* (Risso) from Europe on *Microciona atrosanguinea* Bowerbank, and *R. pulchra* McFarland from the Pacific on *Oplitaspongia pennata* Lambe (Todd, 1981; Cook, 1962). *R. pulchra* has a clear preference for feeding on *O. pennata* rather than some other sponges, and can detect it chemically from some distance (Cook, 1962). By contrast *A. montereyensis* is unable to orientate in a current towards *H. panicea.* If this difference in chemosensory ability occurs also in European species of these genera it would explain why *R. rubra* is usually found close to red sponges while *A. pseudoargus* is very often found some distance from its food (personal observation).

Jorunna tomentosa (Cuvier) also feeds on *Halichondria panicea* (Todd, 1981). It not only resembles its food in color and texture, but its rhinophoral openings and the way the gills are held in an erect circlet closely mimic the openings of the sponge (personal observation). *Aldisa banyulensis* Pruvot-Fol is another red dorid that feeds on sponges, and in addition to color resemblance, it has two depressions on the mantle that resemble sponge oscula. The yellow dendrodorid *Doriopsilla pharpa* Marcus is also highly cryptic on its food sponge *Cliona celata* Grant; the population dynamics of this association have been studied by Eyster and Stancyk (1981). In summary, many, perhaps the majority, of spiculose dorids belonging to the family Dorididae *sensu lato* (including the genera *Doris, Archidoris, Anisodoris, Discodoris, Atagema, Rostanga, Aldisa*) as well as many porostomatous Dendrodorididae (*Doriopsilla, Dendrodoris*) are cryptic in both color and form when in their normal environment amongst their sponge food.

Many eolid nudibranchs are also cryptic when on their hydroid foods for example the brownish *Cuthona amoena* (Alder and Hancock) and *Cuthona concinna* (Alder and Hancock) (Thompson and Brown, 1984). *Cuthona foliata* (Forbes and Goodsir) has conspicuous orange marks, but it is also cryptic amongst hydroids, perhaps because these colors are disruptive marks (Todd, 1981). *Eubranchus exiguus* (Alder and Hancock) and *Tergipes tergipes* (Forskål) are both small animals with mottled patterns of brown, olive and white. They also have large, swollen cerata which resemble the polyps and thecae of calyptoblast hydroids (Giard, 1888). *T. tergipes* has few cerata, and these alternate to left and right, so that it bears a very close resemblance to *Obelia* and *Laomedea* spp. *Catriona gymnota* (Couthouy), several species of *Coryphella*, and *Facelina coronata* (Forbes and Goodsir) all have red diverticula in the cerata and are beautifully camouflaged on their normal food *Tubularia* spp. (Giard, 1888; Todd, 1981). Some species are very restricted in the foods they will eat: *C. gymnota* is very rarely found eating any hydroid other than *Tubularia* (except possibly when newly metamorphosed, see Todd, 1981), and in choice experiments has a specific preference for it (Braams and Geelen, 1953). *Cuthona nana* (Alder and Hancock), another species with pink in the cerata, is virtually confined to a single prey species, the pink *Hydractinia echinata* Fleming which normally lives only on hermit crab shells (Harris *et al.,* 1975; Rivest, 1978). *Dondice paguerensis* Brandon and Cutress is a brownish eolid that is also camouflaged on its prey, the scyphozoans *Cassiopea xamachana* Bigelow and *C. frondoza* Fuwkes (Brandon and Cutress, 1985). A more aberrant eolid, *Glaucus atlanticus* (Forster), has remarkably elongated cerata, probably as an adaptation to buoyancy, and is camouflaged as it floats alongside its blue food, the chondrophores *Velella* and *Porpita* (Thompson and McFarlane, 1967; Thompson and Bennett, 1970). Its upper (ventral) surface is blue while its lower (dorsal) surface is white, so it has reversed countershading (Todd, 1981) like hawkmoth caterpillars (Cott, 1940).

Camouflage occurs in many other opisthobranchs. Most Ascoglossa (= Sacoglossa) are green due to symbiotic photosynthetic plastids which they sequester from their algal food, but *Elysia arena* Carlson and Hoff from the Pacific lives on sand at the base of its food (*Caulerpa* spp.), and instead of being green it is orange-brown (Carlson and Hoff, 1977). Similarly many species of *Aplysia, Bursatella* and *Dolabrifera* are brownish and camouflaged on their brown algal food or on sublittoral rocks. However, *Phyllaplysia zostericola* McCauley lives on the leaves of eel grass (*Zostera marina* L.) where its flattened form, green color and longitudinal white lines resembling veins give it near perfect camouflage (McCauley, 1960).

Cryptic coloration will reduce the chances of a predator finding an animal so long as the animal rests on a background of the appropriate color. Opisthobranchs, however, probably lack color vision and are slow moving, so they could be unable to select an appropriate colored resting place visually. Instead, background color-matching is achieved by sequestering pigment from their food. Abeloos and Abeloos (1932) found that two pigments in *Archidoris pseudoargus* and its food *Halichondria panicea* are identical. While blue pigment was confined to the digestive gland of the nudibranch, yellow carotenoid is found extensively in body tissues and so contributes to the external coloration. Similarly the pink dorid *Hopkinsia rosacea* MacFarland sequesters a pink xanthophyll from its food the bryozoan *Eurystomella bilabiata* Hincks (Strain, 1949; McBeth, 1971). Harris (1973) summarises similar work on other Pacific dorids by Coulom, Anderson and McBeth. The carotenoids that contribute to the red of *Rostanga pulchra* are obtained from its food, but the particular carotenoids present depend on which species of sponge it has recently been eating.

Many species of *Aplysia* change diet and color as they grow, for example *A. parvula* Guilding, when young, is pink and feeds on the pink alga *Asparagopsis taxiformis* (Del.) Trev., but as it grows it migrates to the greenish *Laurencia johnstonii* and it too becomes greenish (Faulkner and Ghiselin, 1983). However, it has not been confirmed that this is due to a direct sequestration of pigment from the food although this is probable. In the Ascoglossa that have symbiotic algae, these are acquired by ingestion and stored in the body tissues so contributing to the animals cryptic color when resting on green algae (Clark and Busacca, 1978; Jensen, 1980).

Background color-matching by acquiring pigment from food works well with species with restricted diets (stenophagy). Euryphagous species (with a wide range of foods) can often change color according to diet. Labbé (1931) reports that *Aeolidiella glauca* (Alder and Hancock) and *Favorinus branchialis* (Rathke) with white digestive glands in the cerata became red after feeding for a day on sea anemones (*Actinia equina* L. and *Anemonia sulcata* Pennant). Tardy (1969) reports that *Aeolidiella sanguinea* (Norman) can be red or brown depending on diet. Haefelfinger (1969) was also able to change the ceratal color of *Spurilla neapolitana* (delle Chiaje) by feeding them with different sea anemones, while Edmunds (1983) observed that pale grey *Aeolidia papillosa* (L.) fed on red *Actinia equina* developed red digestive glands in the cerata. In this way an eolid that moves to a new food quickly acquires the same color as this food and so becomes cryptic. Many eolids can change color in this way, but the range of colors they can acquire varies in different species. The ceratal digestive gland of *Phestilla lugubris* Bergh (= *P. sibogae* Bergh) takes on the color of the part of the coral it has been eating, so it is camouflaged yellow or brown (Harris, 1971a). The closely related *P. melanobrachia* Bergh, however, can develop a much wider range of colors (Harris, 1968, 1971a, b, 1973). *P. melanobrachia* sequesters four of its five types of pigment from the various species of coral it eats. First, red, pink, orange, yellow and black pigments similar to flavones are stored in the digestive gland and can be quickly lost and acquired as an eolid moves from one species of coral to another. A granular black pigment that also accumulates in the digestive gland, and a red carotenoid pigment that is deposited in the epidermis are also obtained from the food but are permanent. Finally, specimens that have fed on the coral *Turbinaria* spp. sequester zooxanthellae in the digestive gland which makes them dark grey. The result of this complex treatment of food pigments is that 95% of *P. melanobrachia* found in the sea on their coral food were cryptic, but a few which had recently moved or had acquired permanent pigments were conspicuous.

Because an eolid that moves on to a new species of food is likely to be conspicuous for a few days one could expect that many eolids could be found that have not had time to adapt to their new diet and so are conspicuous. One reason why so few conspicuous eolids are found is probably because of ingestive conditioning: Hall *et al.* (1982) found that *Aeolidia papillosa* that had been fed on *Sagartia troglodytes* (Price) had a preference for this species of sea anemone when given a choice, but if the same animals were kept on *Actinia equina* they quickly acquired a preference for this anemone over *Sagartia*. Hence an *A. papillosa* that has fed on *Actinia equina*, and has acquired red cerata which make it cryptic on this anemone, will tend to continue feeding on *Actinia equina* even if other anemones are nearby (Edmunds, 1983). Ingestive conditioning also provides a simple explanation for the different food preferences found in experiments on this eolid by various workers (Stehouwer, 1952; Waters, 1973; Harris, 1973; Edmunds *et al.*, 1974; Tardy and Bordes, 1978).

A further way in which opisthobranchs can change color is by differential expansion and contraction of chromatophores. This is the normal method of color change found in fish, reptiles and cephalopods, but it has only been demonstrated in one species of opisthobranch, the shallow-burrowing bullacean *Haminoea navicula* (da Costa) (Edlinger, 1982). When placed on a dark background the dark chromatophores expand over a period of a week to make the animal largely black, while on a pale background they retract so that the animal becomes very pale. This change is presumably mediated through the eyes. Since the change results in color matching of the animal to its background it is reasonable to assume that it has evolved through predator selection for camouflage.

SPECIAL RESEMBLANCE

In some nudibranchs the cryptic adaptations extend beyond coloration and superficial texture (e.g. spicules in dorids) to precise similarities of body form to that of the food. This is special resemblance. Whether special resemblance should be regarded as a form of crypsis or mimicry is a matter of definitions (Vane-Wright, 1980; Edmunds, 1981a), though Robinson (1981) argues that if the animal resembles its model even when separated from it then this should be regarded as mimicry. Some of the examples already mentioned approach this category, for example *Jorunna tomentosa* which has openings dorsally that resemble sponge oscula, and *Catriona gymnota* whose oval red cerata resemble the gonophores of *Tubularia* (personal observation).

Corambid dorids are circular, flattened and lacking a dorsal crown of gills. Their diet appears to be confined to bryozoans, especially *Membranipora.* When resting or feeding on *Membranipora* they are extremely difficult to detect because a cellular pattern on the mantle resembles the bryozoan zooids. Observations on the ecology of *Doridella steinbergae* (Lance) on *Membranipora* spp. growing on *Laminaria saccharina* (L.) at Friday Harbor have been described by McBeth (1968) and Seed (1976), while similar observations have been made on *Doridella obscura* Verrill by Franz (1967) in the west Atlantic. Perron and Turner (1977) have shown that veligers of this latter species can be induced to metamorphose by the presence of its normal food *Electra* (= *Membranipora*) *crustulenta* (Pallas) but not by three other species of bryozoan.

Aegires sublaevis Odhner is another dorid with a special resemblance in color, shape and texture to its food, the sponge *Clathrina coriacea* (Montagu) (Ros, 1976, 1977). Another nudibranch, *Tritonia nilsodhneri* Marcus, lives on the gorgonian *Eunicella verrucosa* (Pallas) which can be pink or white. The nudibranch matches its food in color as well as form with its branched gills resembling the gorgonian polyps (Tardy, 1963; Thompson and Brown, 1984; Just and Edmunds, 1985).

A group of species of nudibranchs that live exclusively on corals has recently been extensively studied. The eolids *Phestilla melanobrachia* and *P. lugubris* are both camouflaged on their normal food coral (Harris, 1968, 1971, 1973). They hold their cerata laterally instead of dorsally so they are inconspicuous when resting on their coral food, but there is no close 'special resemblance' to the host. *P. minor* Rudman, however, has a brown mottled form that is very well camouflaged on the scleractinian coral *Porites somaliensis* Gravier, as well as a white form that matches fish feeding-scars and patches of white coral sand on the *Porites* (Rudman, 1981a). *Cuthona poritophages* Rudman is another eolid that lives only on *P. somaliensis* (Rudman, 1979). It is beautifully camouflaged in color, shape and lateral position of its cerata when the coral polyps are expanded, but is more conspicuous when the polyps are retracted. The aberrant nudibranch *Pinufius rebus* Marcus and Marcus, however, is not merely camouflaged on *Porites somaliensis*, but, like corambids on bryozoans, it closely resembles its food in body form and color markings (Rudman, 1981a). Ridges on its back resemble the edges of individual polyps, white-tipped tubercles occur on both the retracted polyps and on the dorsum of the nudibranch, and there are white-tipped cerata of similar color, size and shape to the coral tentacles.

Just as species of *Phestilla* are associated with scleractinian corals, so species of the eolid genus *Phyllodesmium* appear to be associated with alcyonarians. Some appear to have simple camouflage, but in others the resemblance to a specific alcyonarian extends to color, shape of body and shape of cerata (Rudman, 1981b). *P. poindimiei* (Risbec) bears a very close resemblance to its food, the orange soft coral *Telesto* sp., *P. hyalinum* Ehrenberg has an even more perfect resemblance to a yellowish species of *Xenia,* and *P. cryptica* Rudman has yellowish or bluish knobbed cerata exactly matching the color and knobbed tentacles of the various forms of *Xenia* on which it lives. Species of the aeolidiid genus *Aeolidiopsis* also feed and have a specific resemblance to their food, the colonial zoantharian *Palythoa* spp., while the aberrant, flattened arminacean *Doridomorpha gardineri* Eliot is quite remarkably camouflaged on the coral *Heliopora* sp. (Rudman, 1982a). However, by far the most extreme adaptation in terms of mimicry of a specific food is that of the eolid *Cuthona kuiteri* Rudman from Australia whose cerata have tiers of tentacles closely resembling the tentacles of the aberrant hydroid *Zyzzyzus spongicola* (von Lendenfeld) whose polyps project from sponges (Rudman, 1981c).

Although *Cuthona kuiteri* is clearly a hydroid mimic with a 'special resemblance' to *Zyzzyzus*, it is not easy to decide whether some of the other nudibranchs are simply cryptic or have a special resemblance. The distinction is in terms of predator perception: if predators overlook a nudibranch because it merges with its background, then the nudibranch is cryptic; but if predators ignore it because they mistake it for a coelenterate they do not eat, then the nudibranch has a special resemblance to the coelenterate.

APOSEMATIC (WARNING) COLORATION

A number of species of opisthobranch mollusc are highly colored and conspicuous in their natural environment and it has been suggested that the following have warning coloration: *Limacia clavigera* (Müller), *Polycera quadrilineata* (Müller), *Eubranchus tricolor* Forbes, *Facelina coronata* (Forbes and Goodsir) (Hecht, 1896); species of Chromodorididae including *Chromodoris reticulata* (Pease) and *C. diardii* (Kelaart) (Crossland, 1911); and many eolids (Garstang, 1889; Herdman, 1890; Herdman and Clubb, 1890). Garstang (1890) and Hecht (1896) were, however, well aware that not every brightly colored nudibranch is necessarily aposematic, and they pointed out that some are actually cryptic in their normal environment; but they both believed that some species are conspicuous and do have warning colors. More recently Ros (1974) has drawn attention to groups of brightly colored aposematic species of chromodorid, while Harris (1973) and Todd (1981) mention species that are also probably aposematic such as the tropical *Phyllidia varicosa* Lamarck and the West Pacific *Triopha carpenteri* Stearns and *Diaulula sandiegensis* (Cooper). Thompson (1960) cautioned against the simplistic view that cryptic species are palatable while aposematic ones are not, and Edmunds (1974) argued for more experimental evidence before one should conclude that aposematic coloration really does occur in opisthobranchs.

A recent definition of aposematism has been given by Edmunds (1974): "Animals which have dangerous or unpleasant attributes, and which advertise this fact by means of characteristic structures, colours, or other signals so that some predators avoid attacking them, are said to be *aposematic*, and the phenomenon is called *aposematism*".

If this definition is accepted then in order to demonstrate aposematic coloration it is necessary to establish:

1. that a species is conspicuously colored or advertises itself in some other way;
2. that it is sufficiently noxious that some predators will not eat it;
3. that some predators avoid attacking it because of its color (or other signal);
4. that this color or other signal provides better protection to the individual or to its genes than would other (e.g. cryptic) signals.

Only if all four of these criteria are met will there be selective advantage in the warning signals. If criterion 4 is not met then there can be no advantage in an animal being conspicuous: it would be better protected if it were cryptic and warning colors could not evolve. Criterion 1 is well documented (see above). Criterion 2 is also well established; Crossland (1911), Crozier (1916) and Thompson (1960) have all demonstrated that a variety of species of brightly colored nudibranchs are unpalatable to fish. The molluscs were usually dropped into aquaria or the sea whereupon fish attacked them as they fell through the water. Almost every mollusc, however, survived even though it may have been ingested and spat out several times before reaching the substrate, after which it was usually ignored. Criterion 3 was not established in these experiments, perhaps because the stimulus to snap at any potential food object falling through the water is so powerful that it overrides any possible learned aversive response (Edmunds, 1974). Most shallow-water fish have color vision and are capable of learned responses, but so far only very preliminary experiments have been carried out to test if fish can learn not to attack nudibranchs that they have, a few minutes earlier, found to be distasteful (Edmunds, 1974). Nevertheless, since birds, amphibians, reptiles and octopus can quickly learn to avoid conspicuous but noxious prey it is probable that fish can do so as well (evidence summarized in Edmunds, 1974). Criterion 4 has not been demonstrated in any marine predator.

Predators can acquire an aversive response to aposematic prey in two distinct ways: first, by learning (negative conditioning); and second, by a long period of exposure to noxious prey over many generations during which they evolve an innate aversive response to certain specific signals (see e.g. Smith, 1975, 1977).

It is reasonable to conclude that aposematic coloration probably does occur in many nudibranchs, although it remains unproven. The species in which it is most likely to occur are the chromodorids, phyllidiids and perhaps some eolids. There is some indirect evidence that supports this conclusion. Where aposematism occurs and where the relevant predators have to learn by experience to avoid the warning colors, then it will pay the various aposematic species to evolve similar color signals (müllerian mimicry). In this way predators will have to sample (and perhaps kill) a much smaller number of individuals before they have established their conditioned avoidance response than if there were several different color signals, and the loss to prey while they learn will be spread among several species. Examples of nudibranchs that are not closely related taxonomically but which share a common pattern have been documented by Ros (1974, 1977). Details are given below, but the occurrence of what appears to be müllerian mimicry supports the hypothesis that these animals have warning colors.

Another possible example of warning coloration is described by Thompson (1985). He reports that the dorid *Peltodoris atromaculata* Bergh and the pleurobranchid *Berthella stellata* (Risso) are both conspicuous to divers in the Mediterranean, and that they are very variable in the pattern of dark and white markings. If warning coloration occurs one can predict that the pattern should be relatively constant in any one population since then predators need only learn one pattern in order to avoid all individuals. If the population is variable, or polymorphic, then predators might have to learn several patterns, and hence would sample many more individuals before they could learn to avoid them all. This argument supports the view of Ros (1976) that *P. atromaculata* is actually cryptic with disruptive coloration and is not conspicuous. Clearly, as Thompson (1985) indicates in his note, more information is required on the variation in these species both within and between populations. Perhaps they are monomorphic and aposematic in some populations but polymorphic and cryptic in others depending on the predators in each locality.

Another problematical example is the eolid *Eubranchus farrani* (Alder and Hancock). This species is typically brilliant orange-yellow and white and so is relatively conspicuous on the dull colored hydroids which it eats. However, Edmunds and Kress (1969) showed that the population at Plymouth is polymorphic with four color forms: orange and white; orange; orange and brown; and white. There may be additional color morphs elsewhere (Thompson and Brown, 1984; Just and Edmunds, 1985). Once again, it is difficult to explain the occurrence of so many color morphs if the colors are aposematic, and one almost begins to take seriously the view of Crozier (1916), based on *Hypselodoris zebra* Heilprin, that the color is fortuitous and the result of selection pressures for some other character that just happens to be associated with color.

There are, however, several possible explanations of color variation in *Eubranchus farrani*. For example, the different frequencies of the various morphs in different populations could reflect different species of predators. It could be that the typical orange-yellow and white form is selected for in areas where predators quickly learn to avoid this pattern either by attacking and rejecting *E. farrani* or by attacking a similarly colored species such as *Polycera quadrilineata*. In areas where it is rare and where no müllerian mimics occur, or where the relevant predators fail to learn not to attack it, it could be more advantageous to be cryptic (dark brown for example). There could also be areas where it pays to have several color morphs because predators could be hesitant to attack novel prey. This is apostatic selection but it is more likely to occur in cryptic than in aposematic animals (Clarke, 1962; Edmunds, 1974).

A third problem is posed by brilliantly colored but rare species. *Polycera elegans* (Bergh) is orange with blue spots and was found only six times in 66 years (Edmunds, 1961) despite being large and very conspicuous. It has been found more frequently in recent years by divers, but it remains a local and uncommon species except at Lundy where it is sometimes abundant (Thompson and Brown, 1984). The problem is how a scarce species can benefit by evolving warning colors. Because it is rare, predators are unlikely to evolve an innate aversive response, so they must learn by experience to avoid it. But the experience of a predator sampling a noxious prey can be fatal to the prey even if it is eventually rejected by the predator. For such prey animals warning colors will only benefit other individuals than the one sampled, and so aposematism can only evolve through kin selection (Harvey *et al.*, 1982). This is unlikely to occur in rare species: it would pay them to be cryptic as this would reduce the numbers killed while the predators learn, and it could not occur in species with planktotrophic larvae since the individuals benefitting from a predator's learned aversion would not necessarily be genetically related to the individual that died. An alternative explanation is that rare aposematic species are tough enough to survive sampling by a predator, so that the individual that is attacked is the one that benefits from the predator's learned aversion (Jarvi *et al.*, 1981; Wiklund and Jarvi, 1982).

BATESIAN AND MÜLLERIAN MIMICRY

Ros (1976, 1977) has suggested five groups of mimetic nudibranchs which he terms aposematic or mimetic circles. The mimicry could be either batesian or müllerian. In batesian mimicry one or more palatable species mimic an aposematic 'model', whereas in müllerian mimicry several aposematic species share the same color pattern. Ros's first mimetic group are blue and gold chromodorids in which the mantle is largely bright blue with orange, yellow or white markings. In the Mediterranean this group includes *Hypselodoris gracilis* (Rapp), *Mexichromis tricolor* (Cantraine), *H. messinensis* (von Ihering), *Chromodoris krohni* (Verany), *H. valenciennesi* (Cantraine) and *H. bilineata* (Pruvot-Fol). Some of these species occur also on the Atlantic coast of Africa and the Bay of Biscay where additional blue chromodorids include *H. tema* Edmunds from Ghana, *H. cantabrica* Bouchet and Ortea from Biscay and *H. webbi* (d'Orbigny) from the Canaries (Bouchet and Ortea, 1980; Edmunds, 1981b). Chromodorids are well known to be unpalatable to many fish (Crossland, 1911; Crozier, 1916) due to a variety of chemicals (summarized by Schulte and Scheuer, 1982; Thompson *et al.,* 1982; and Faulkner and Ghiselin, 1983), and they have large glands that characteristically exude a secretion when they are attacked (Edmunds, 1981b; Rudman, 1984). Some of these species could simply have evolved from a similarly blue and gold species in the recent past and so their colors are still very similar, but others belong to different genera and are likely to be the result of convergent evolution. Young *H. bilineata,* young *H. gracilis* and adult *M. tricolor* for example have almost identical patterns (Haefelfinger, 1959; Edmunds, 1981b). Rudman (1982b, 1983, 1985, 1986) has described several other similar groups of chromodorids which have evolved similar patterns convergently.

Another mimetic group described by Ros (1976, 1977) is of white nudibranchs with red, orange or yellow markings: *Chromodoris elegantula* Philippi and *Diaphorodoris papillata* Portmann and Sandmeier have red spots and a yellow border; *Crimora papillata* Alder and Hancock, *Ancula gibbosa* (Risso), *Trapania maculata* Haefelfinger, *Polycera quadrilineata* and *Limacia clavigera* have orange or orange-yellow spots or papillae, and *Calmella cavolinii* Verany has red papillae. To these can be added the eolid *Eubranchus farrani* with orange spots, and, in northern Europe, *Polycera faeroensis* Lemche with yellow spots. Ros suggests that this group have evolved towards a well protected eolid such as *Calmella cavolinii* and so presumably some are batesian and some müllerian in their relationship. However, there is no evidence that eolids are any more noxious than the dorids in this group, many of which have defensive glands in dorsal papillae. It is therefore possible that this is another müllerian mimetic group of species, although whether predators can generalise across the entire group, or whether they recognise *Chromodoris elegantula* and *D. papillata* as one type of noxious prey and the remaining dorids as another is not known.

Conclusions on the nature of these mimetic groups must be tentative since there is no information on likely predators and how these perceive nudibranchs, but the fact that such groups exist implies selection for similar color patterns and hence mimicry. Most species are probably müllerian mimics, but some could be batesian, and some could be batesian with respect to one predator but müllerian to another.

FLIGHT AND FLASH COLORATION

Some terrestrial animals increase their chances of escaping by means of flash colors (Cott, 1940; Edmunds, 1974). Although experimental proof is lacking, it is thought that predators pursue a conspicuous color on the fleeing prey, but when the prey stops and conceals this 'flash' color, the predator is left baffled, and could give up the search.

Apart from the Pteropoda (which have not been included in this review) the majority of opisthobranchs are slow moving benthic animals, quite incapable of rapid escape movements. Even species that swim do so comparatively slowly (Farmer, 1970; Thompson, 1976), but this can be sufficient to enable them to escape from slow moving predators. *Tritonia diomedea* swims in response to chemicals released by the starfish *Pycnopodia helianthoides* (Willows, 1967), and several other nudibranchs respond to rough handling by swimming (summarized by Thompson, 1976).

There is one nudibranch which possibly has flash coloration: the Indo-Pacific dorid *Hexabranchus sanguineus* Rüppell and Leuckart. As *Hexabranchus* swims it exposes bright red and white spots on its dorsal surface, but when it comes to rest the edge of the mantle is rolled up, concealing these markings, and the mollusc is then very often cryptic (Edmunds, 1968b). However, there is no published record of a predator pursuing swimming *Hexabranchus*, let alone being confused by its color marks vanishing when it stops swimming.

DEIMATIC BEHAVIOR

Deimatic or frightening behavior is a display that intimidates a threatening predator causing it to hesitate or back away (Edmunds, 1974). Some deimatic behaviors are genuine warnings that an animal is noxious, so they reinforce the primary aposematic defence (as with the skunk *Spilogale putorius*), but others are bluff (e.g. the eyespots of the hawkmoth *Smerinthus ocellatus*). There are several possible examples of deimatic behavior in opisthobranchs. It is well known that when eolids are molested most species contract the rhinophores and extend and wave the cerata vigorously (see e.g. Edmunds, 1966a). Eolid cerata are often brightly colored and this adds to the conspicuousness of the display. Janolids and stiligerid ascoglossans have similar behavior (personal observation). Another example of deimatic behaviour is in *Hexabranchus sanguineus* (= *H. marginatus*) (Edmunds, 1968b, 1974). The crawling animal is cryptic on many parts of the coral reef, but when attacked it responds by unrolling its dorso-lateral mantle thereby exposing bright red and white marks. After a few seconds the mantle margin is rolled up and the mollusc again becomes cryptic. Some chromodorids with wide, folded mantles can have similar behavior although these have not been carefully studied.

Lobiger souverbiei Fischer and *L. viridis* Pease can also show deimatic behaviour (K.B. Clark and R.C. Willan, respectively, pers. comm). These ascoglossans have four erect flaps on the body which can be autotomised but which are normally held curled over the dorsal surface. When the animal is disturbed, these are unfurled to display vivid red spots on their inner, upper surfaces. After one to two seconds *L. viridis* refolds the flaps and the spots disappear. Species of *Plocamophorus* (Polyceridae) have knobbed protuberances (globes) on the body. In *P. imperialis* Angas these globes are reported to emit a luminous fluid when the animal is molested (Willan and Coleman, 1984).

Although all of these examples appear to be deimatic, in no case has the behavior actually been shown to intimidate predators.

DEFLECTION OF AN ATTACK

Some animals have behavior that diverts predators away from themselves or their young, or they can have deflection marks that direct attacks to either an expendable or a noxious part of the body (Edmunds, 1974). Eolids, some dorids, arminids, dendronotids and ascoglossans have ceratal papillae which they often wave conspicuously when attacked, and which can be autotomised and later regenerated. The cerata are often brightly colored and so a predator which attacks is likely to get a mouthful of these while the nudibranch crawls away unharmed. The cerata also contain defensive structures concentrated near their tips: nematocysts in eolids and glands containing toxic secretions in some eolids, dorids, arminids, dendronotids and ascoglossans (Edmunds, 1966a, b, 1974; Ros, 1976; Harris, 1973; Jenson, 1984). Again, there is no proof that colored cerata function in this way, but by analogy with deflection marks in other animals, it is probable.

INTRASPECIFIC SIGNALS

If visual stimuli play a part in intraspecific behavioral interactions of opisthobranchs, then these molluscs must have good eyes. However, opisthobranch eyes are so simple in structure (summarised in Hyman, 1967; Franc, 1968) that it is virtually certain that they are unable to form an image of, for example, the color pattern of another individual. Hence there is no evidence that colors in opisthobranchs have an intraspecific signalling function.

FORTUITOUS COLORS

Among opisthobranchs there are a few deep sea species but there is very little information on their color in life. Most published accounts are of animals collected on a deep sea expedition when no notes of the living animals were made. The preserved specimens usually lack pigment but it is not known if this is because they were white or because the original pigment has dissolved out. Nevertheless, a careful search of the literature does suggest that opisthobranchs from abyssal depths lack pigment. Bouchet (1975) refers to the color of 14 out of 30 species of abyssal Atlantic opisthobranchs, and the color of two of the remaining 16 is known from other sources. Out of 10 species dredged from depths exceeding 1175 m, eight had white shells and two yellow shells. Of six species from shallower areas, 140-1080 m, three were white, one yellow, one red, and one white with darker dots [*Philine scabra* (Müller)]. The red species, *Gastropteron rubrum* (Rafinesque), and *Philine scabra* also occur in much shallower water where their color is likely to be visible, and *G. rubrum* also swims in shallow water (Haefelfinger and Kress, 1967). These data suggest that shallow water benthic species are more often pigmented than abyssal species, though it is far from conclusive. Bouchet (1977) describes a further 16 species of deep sea opisthobranchs: five are variously colored (red, violet, brown, olive, and black spotted) but the rest are uniformly either white or yellow. The colors could be fortuitous, or they could have a function in shallower water as with *G. rubrum*, but more information is required on their depth range. Another pointer is given by Marcus and Marcus (1969). They describe two species of *Philine* with brown body color, *P. lima* (Brown) and *P. thurmanni* Marcus and Marcus. *P. lima* was collected from 200 m, but it occurs elsewhere in only 4 m of water, so if it is ever exposed on the surface of the sea bed its brown color could provide camouflage. *P. thurmanni* occurs from 70 to 4116 m and can be either white or brown. Most of the brown ones were from shallower depths whereas all four white ones came from depths exceeding 4000 m. The authors suggest that the difference in color can be due to different preservatives, but I suggest that it is more likely that the brown is of selective advantage in regions where light penetrates to the sea bed, but white is favored by selection at greater depths.

Animals that show adaptations to cave life are typically freshwater or terrestrial, and no opisthobranchs are known that live only in caves. [*Discodoris cavernae* Starmühlner, a brown dorid described by Starmühlner (1955) from caves near Naples, is considered by Schmekel and Portmann (1982) to be conspecific with the much more widely distributed *D. indecora* Bergh despite some unusual features in its reproductive system.]

There are, however, a substantial number of burrowing opisthobranchs, particularly in the Bullacea. These glide through sand or mud using the front part of the body as a plough, and with a copious supply of mucous carrying particles of sand back over the body surface. Many of these animals burrow close below the surface and their dorsal mantle is frequently visible above the sand, so there could still be an advantage in having pigmentation dorsally for camouflage as a defence against predators. Other species burrow more deeply and only rarely come to the surface, and we might predict that in these animals energy saving considerations should lead to the loss of pigment so that they would be colorless or white.

I have tried to test these predictions by examining the British fauna as summarised by Thompson (1976) and Thompson and Brown (1984), supplemented by reports of burrowing opisthobranchs from elsewhere. First there are many burrowers that are as strongly pigmented as are surface living and epizootic forms. If color is fortuitous then some at least of these species should be deep burrowers which rarely come to the surface. Burrowing nudibranchs occur in the genera *Armina, Cerberilla, Pseudovermis* and possibly

Embletonia. There are no comprehensive descriptions of the burrowing and feeding habits of these animals, but *Cerberilla* (Aeolidacea) and *Armina* (Arminacea) feed on prey which projects from the substrate so there is presumably advantage in being camouflaged when feeding. Little is known of the habits of *Pseudovermis* and *Embletonia*, but *Pseudovermis* is a member of the interstitial fauna. These species lack pigment though the gut may be colored (brown or vermilion in *Embletonia*, depending on diet), and this is likely to improve camouflage when eating hydroids on the surface of the substrate.

Species of the Philinoglossacea also have some pigment (Thompson, 1976), but it is not known how deeply they burrow nor how often they live on the surface.

Pleurobranchaea spp. (Pleurobranchacea) also burrow, but in my experience they are normally only partly buried as they plough through sand; hence their colors can be interpreted as being cryptic.

In the Bullacea colored species occur in the genera *Bulla, Acteon, Haminoea, Atys, Roxania, Bullina, Micromelo, Hydatina, Runcina* and in the Aglajidae. However, species in the last four of these genera and in the Aglajidae spend much time on the surface instead of burrowing, so their coloration is likely to be cryptic or possibly aposematic. In the Runcinoidea for example, the European *Runcina coronata* (Quatrefages) is black and *R. ferruginea* Kress is red, while *R. katipoides* Miller and Rudman from New Zealand is striped. All three species appear to live on the surface of mud or algae and there is no record of their burrowing (Thompson, 1976; Rudman, 1971a). The other bullacean genera listed above include species which burrow. *Haminoea, Bulla* and *Quibulla* spp. plough through mud and sand secreting a mucous tube (Rudman, 1971a, b). Sand adhering to the mucus on the dorsal surface partially conceals the animal from above even though it may be crawling only a millimetre or two below the surface. However, these are all herbivores and are exposed to view when browsing on algae. *Haminoea hydatis* (L.) and *Roxania utriculus* (Brocchi) are also reported to swim (Thompson, 1976) where their coloration may be of protective value. The Acteonidae are carnivores typically feeding on polychaete worms (Hurst, 1965; Rudman, 1972a). *Acteon tornatilis* L. with a creamy white body and pink, mauve and white shell, burrows deeply but also comes to the surface from time to time (Fretter and Graham, 1954). Yonow (personal communication) records that it spends much time crawling on the surface of the sand at low tide. Although she reports that it is not particularly well camouflaged, there is probably selective advantage in being pink rather than white. *Pupa kirki* (Hutton) also burrows deeply but frequently returns to the surface and rests with its front end protruding (Rudman 1972a). In this position its drab color camouflages it.

The second group of burrowing opisthobranchs is either translucent or white to cream in color, but entirely lack colored pigment. Where a visible shell is present it is usually white or transparent. British species with these characters include *Diaphana minuta* Brown, *Retusa* spp., *Rhizorus acuminatus* Bruguière, *Cylichna cylindracea* (Pennant) and *Philine aperta* (L.). With the exception of *P. aperta* nothing appears to be known of whether these animals burrow deeply or shallowly, nor whether they frequently live on the surface. *P. aperta* can burrow deeply, but it also ploughs just below the surface where its white color is invisible because cilia and mucus carry a film of mud over its dorsal surface (Brown, 1934). It feeds on burrowing animals including the polychaete *Pectinaria* (Hurst, 1965). Two similar white philinids from New Zealand have also been studied, *Philine angasi* Crosse and Fischer and *P. auriformis* Suter (Rudman, 1972b). These both feed on burrowing bivalves, and *P. angasi* is apparently unable to swallow prey on the surface. Hence practically the entire life of these species is spent buried. Pigment can clearly have no protective value to them so the fact that they are white supports the hypothesis that conservation of energy is more important than any biochemical process which results in the formation of pigment as a biproduct. A possible exception to this conclusion is *Scaphander lignarius* (L.) which is yellowish and is thought to live and feed in a similar way to *Philine aperta* (Hurst, 1965). However, there is no good study of its burrowing habits. *Ringicula buccinea* (Brocchi), another white bullacean, has a large, thick external shell that is also white. It burrows just below the surface maintaining contact with the aerated water above by means of a short funnel (Fretter, 1960), but it is not clear how often it is exposed while burrowing.

Thus, although our knowledge of the ecology and behaviour of burrowing opisthobranchs is very superficial, the available evidence suggests that pigment in colored species is of protective value, that lack of pigment is a result of energy conservation in situations where color has no protective value, and that the occurrence of fortuitous colors in opisthobranchs remains unproven.

DISCUSSION

In this review I have tried to summarize the evidence concerning the functions of color in opisthobranch molluscs. There is a wealth of circumstantial evidence supporting the view that many species are cryptic or have specific resemblances to sessile prey, but there the hard evidence ends. There is tremendous scope for experimental (as opposed to anecdotal) study of the adaptive role of coloration in opisthobranchs. The subject of warning coloration requires thorough investigation using appropriate species of fish as predators, and the mimetic groups of nudibranchs pose a more formidable investigative problem. Are these müllerian or batesian or perhaps a mixture of the two with respect to different predators? Polymorphic species raise further questions: are these simply cryptic with polymorphism a defence against predators which hunt by acquiring search images of common prey (Edmunds, 1974)? Or are they aposematic in which case the role of polymorphism is obscure? Or are some morphs cryptic while others are aposematic? Experimental studies are also required on flash behavior, deimatic displays and deflective colors. Finally, on the question of fortuitous colors, I would like to suggest two areas that might repay further study. First, the observation that many burrowing and deep sea opisthobranchs are yellow rather than white requires an explanation; and second, the detailed and often very intricate color pattern of many opisthobranchs raises the question of whether this level of detail is of functional significance.

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ON DEVELOPMENTAL PATTERNS OF OPISTHOBRANCHS

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ABSTRACT

Data from recent publications on developmental characteristics of opisthobranchs are added to prior compilations to arrive at a broad picture of opisthobranch developmental patterns. Egg diameters vary from 40 to 380 μm, with a modal size of about 75 μm; this distribution is similar for each of the larger opisthobranch orders alone. In general, planktotrophic larvae arise from eggs smaller than 130 μm, but a few species with lecithotrophic larvae or even directly developing juveniles fall below this limit. Lecithotrophic larvae develop from eggs as large as 220 μm, but most from eggs less than 185 μm in diameter. All larger eggs produce crawling juveniles at hatching. Positive correlations link egg size and hatching-shell size, but there is no correlation between hatching size and settling-shell size nor hatching size and larval duration. Type II larval shells are larger than Type I shells from eggs of equal diameter. Until metamorphic competence, the duration of larval existence is temperature dependent for both larval types, and for planktotrophic larvae is effected by phytoplankton abundance. Once larvae are metamorphically competent, the duration of their larval period is determined by the availability of appropriate settlement substrata.

Size of recently metamorphosed juveniles shows low correlation with egg diameter ($r^2 = 0.29$), but does not exceed 500 μm length for any species with larval development, whether planktotrophic or lecithotrophic. Only direct development with little retention of larval characters produces hatching juveniles between 0.5 and 1.0 mm long. We conclude that opisthobranch larval development is regulated by strong phylogenetic constraints and that selective pressures leading to non-planktotrophic development have probably not been the same across all opisthobranch taxa. Early juvenile mortality can be a strong force favoring high larval numbers, even in species with lecithotrophic larval development.

The ecology and evolutionary patterns of reproduction and development in opisthobranchs have been the subject of intense interest in recent years, as reflected by the number of general reviews of the subject that have appeared (Thompson, 1976; Bonar, 1978; Hadfield, 1978; Hadfield and Switzer-Dunlap, 1984; Todd, 1981, 1983). Our goal here is not to analyze again all the material covered by the recent reviews, but rather to focus on the developmental patterns, or modes, exhibited by opisthobranchs and to attempt to arrive at generalizations regarding their evolutionary implications and limitations. In so doing, we have updated and utilized the data base compiled from the literature by Hadfield and Switzer-Dunlap (1984). Only publications not included in the earlier bibliography are cited in the present paper. Species not considered by Hadfield and Switzer-Dunlap are listed in Table V. Several important points must be made about the data set. (1) The literature is variable in its reliability. Authors often differ in their reporting of egg diameters and other developmental parameters for the same species. Occasionally, from paper-to-paper, even single authors give widely differing numbers. (2) We have used some data in ways authors never intended. For instance, we have extrapolated measurements from drawn and photographed figures, often when the figures didn't include clear magnification scales and they had to be deduced from the texts. (3) Not all parameters mean the same thing in all taxonomic groups; juvenile length (used as a measure of post-metamoprhic size) is elastic and may represent a very different proportion of body mass in different opisthobranch taxa. (4) Where authors gave only ranges for parameters of interest (e.g. egg diameter, rearing temperature) we have substituted a single mid-point value. (5) For eight species, different authors have presented very

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different data for species of the same name; we have considered these to be separate species in our analyses. (6) We have selected references that provided the most complete information about each of the 418 species of opisthobranchs considered in this review. Thus some published data for a species may have been utilized and other data not. It is hoped that the large sample sizes available for some of these parameters (e.g. egg diameters were available for 369 species) more than outweigh the effects of these numerous sources of uncertainty.

As has often been stated, benthic marine invertebrates achieve recruitment to juvenile-adult populations in three basically different ways. First, there are those species that release their young as swimming larvae which must feed for some period of time in the plankton before they are competent to assume the adult form and habitat. These are generally referred to as "planktotrophic-pelagic", "indirect-planktotrophic", etc. Second are species which reproduce as above, except that their larvae, which usually swim for a short period of time before assuming the adult habitat and form, do not need to feed before metamorphosing; we refer to these species variously as ones with "indirect-lecithotrophic development" and "pelagic-non-feeding larvae." Finally, there are those species which release their young as small replicates of themselves, directly into the parental habitat. This mode of reproduction, usually referred to as "direct development", could be accomplished by viviparity, ovoviviparity, brooding, or depositing zygotes in external capsules for development. The second group, the lecithotrophic larviparous forms, overlap both of the others: the direct developers in not requiring external nutrition to achieve the benthic stage (in fact the direct developers, too, are lecithotrophic), and the planktotrophs in having a genuine larval stage that must find a habitat suitable for metamorphosis, growth and reproduction.

The successful result of the developmental process for any species is the production of a juvenile organism, usually residing in the definitive habitat of the species. Thus one measure of evolutionary success is how assuredly a species accomplishes this event. The time required to reach the juvenile stage varies among these developmental modes in several ways, the first being the time spent in pre-hatching development. This period is generally shortest for the planktotrophic forms and longest for the direct developers. The duration of pre-hatching development varies with egg size (the larger the egg, the longer the pre-hatching period) and with temperature (the colder the temperature, the longer the pre-hatching period).

The duration of pre-juvenile development also varies during the larval phase. This phase is longest for the planktotrophs, is usually much less for the pelagic-lecithotrophs, and is non-existent for the direct developers. For both pelagic groups, the duration of the planktic period is sensitive to temperature, and for the planktotrophic forms, duration is also affected by food quality and abundance.

The generalizations so far outlined pertain to nearly all marine invertebrate groups. Our goal here is to look specifically at the opisthobranch mollusks and attempt to arrive at explanations for the differing durations of development, as well as to produce some generalizations about how pelagic larvae find their prospective juvenile habitats.

WHERE LARVAE SETTLE

Before discussing "when larvae settle", we first consider where larvae settle, partly because it is simpler to address and partly because it contributes to an understanding of the first question. In this discussion we deal only with species that actually have a larva, either planktotrophic or lecithotrophic. Species with direct development will obviously "settle" in the place where they hatch, presumably in the same habitat where their parents existed and deposited their eggs.

It is axiomatic that for a larva to survive and grow to a successfully reproducing adult, it must settle and metamorphose in a place where: (1) food is available, (2) there is refuge from predators, and (3) others of its kind are around with which to mate. Usually such habitats are narrowly and discontinuously distributed in the sea, so that a larva must be able to locate and recognize them at a time when it is capable of metamorphosing. This is accomplished in most opisthobranch larvae through a developmental-behavioral shift that brings about swimming near the bottom (e.g. Miller and Hadfield, 1986) and then by sensing chemical and/or physical attributes of appropriate sites, settling onto such sites and metamorphosing there (Hadfield and Scheuer, 1985).

The degree of specificity of the settlement cue has been found to vary considerably, but, in a general sense, predictably (see Tables 1 and 2), as follows. Species with highly specific food requirements (i.e. feeding on only one or a small group of species) which are sessile and patchy in distribution, will metamorphose only in response to chemical cues arising from the food substance, usually a colonial animal or an alga. Examples include coral-, hydrozoan-, and bryozoan-feeding nudibranchs, and algal-feeding sacoglossans and sea hares. Species with either less specific food requirements or motile prey usually settle in response to general characteristics of the environment in which their prey and other members of their own species live. Examples include carnivorous cephalaspideans and several aeolid nudibranchs that feed on a variety of fouling community organisms [*Hermissenda (=Phidiana) crassicornis* (Eschscholtz)] is a good example (Harrigan and Alkon, 1978).

Both soluble chemical cues and absorbed ones requiring larval contact have been implicated in inducing settlement and metamorphosis in different opisthobranch species. In our laboratory, work has focused on the settling requirements of the coral-feeding aeolid nudibranch, *Phestilla sibogae* Bergh. Lecithotrophic larvae of this species settle only in response to a soluble chemical cue emanating from the adult prey, members of the scleractinian coral genus *Porites.* The inducing substance is a small (<500 dalton), water soluble molecule (Hadfield and Scheuer, 1985). It is constantly leaching from the coral in the field, but is probably concentrated enough to elicit metamorphosis only in the coral heads themselves. To our knowledge, no other opisthobranch

Table 1. Settlement requirements of opisthobranchs with planktotrophic larvae.

Species	Adult Food	Settlement Requirement	Reference
Nudibranchia			
Doridacea			
Doridella obscura Verrill	*Electra crustulenta* (Pallas)	same[1]	Perron and Turner (1977)[2]
D. steinbergae (Lance)	*Membranipora villosa* Hincks	same	Bickell and Chia (1979)[2]
Onchidoris bilamellata (Linnaeus)	barnacles	same	Todd (1981)[2]
O. muricata (Müller)	*E. pilosa* (Linnaeus)	same	Todd and Havenhand (1985)
Archidoris pseudoargus (von Rapp)	*Halichondria panicea* (Pallas)	same	Todd and Havenhand (1985)
Rostanga pulchra MacFarland	*Ophlitaspongia pennata* (Lambe)	same	Chia and Koss (1978)
Aeolidiacea			
Phidiana crassicornis (Eschscholtz)	various cnidarians and tunicates	*Obelia* spp.	Harrigan and Alkon (1978)
Phestilla melanobranchia Bergh	*Tubastraea coccinea* Lesson	same	Harris (1975)[2]
Dendronotacea			
Melibe leonina (Gould)	various crustaceans, etc.	surface	Bickell and Kempf (1983)
Tritonia diomedea Bergh	*Virgularia* sp. and other pennatulaceans	surface (enhanced by *Virgularia* sp.)	Kempf and Willows (1977)[2]
Cephalaspidea			
Acteocina canaliculata (Say)	? small molluscs	surface	Franz (1971)[2]
Haminoea solitaria (Say)	uncertain; microalgae? molluscs?	1º film from adult habitat	Harrigan and Alkon (1978)[2]
Sacoglossa			
Alderia modesta (Lovén)	*Vaucheria* sp.	? surface +/- *Vaucheria*	Seelemann (1967)[2]
Elysia chlorotica (Gould)	filamentous green algae	?	Harrigan and Alkon (1978)[2]
Anaspidea			
9 Aplysiid species	each specific to a few algae	same	Switzer-Dunlap and Hadfield (1981)

[1]settlement substratum is the same as adult food; [2]cited in Hadfield and Switzer-Dunlap, 1984.

settlement factor has been explored as to its chemical structure, but evidence appears to implicate non-soluble cues in other species (e.g. *Rostanga pulchra* MacFarland; Chia and Koss, 1978). Numerous studies on *Aplysia* species in our lab have failed to produce evidence for soluble inducer molecules (unpublished data).

Evidence gained from studies on *Phestilla*, as well as on other marine gastropods (e.g. the abalone; Morse *et al.*, 1980) and members of other phyla (sea urchins, for instance), strongly implicates specific external larval receptors that are activated by specific chemical substances in the environment by molecular fitting (the hormone-receptor model fits well). Once larval receptors are activated, the signal is transmitted by neural pathways (excess potassium alone can induce many invertebrate larvae to metamorphose), and the morphogenetic events of metamorphosis result from the action of well known neurotransmitter- and hormone-like substances (choline-containing compounds and catecholamines) on transforming tissues (Hirata and Hadfield, 1986; Yool *et al.*, 1986).

Larvae that respond to general cues have been reported to require either: (1) only a solid surface upon which to metamorphose; (2) a surface coated with a so-called primary film of marine bacteria and fungi and their extracellular exudates; or (3) a surface plus a primary film derived from micro-organisms specific to the appropriate adult habitat (Tables 1 and 2). It is doubtful if any larvae metamorphose on genuinely clean glassware, and probably most larvae observed to metamorphose in culture were doing so in response to at least a primary film; such films develop in less than 24 hours in sea water, particularly in warmer waters (Zobell and Allen, 1935).

All species have been evolutionarily molded to assure that their offspring that survive to metamorphic competence have a good chance of correctly finding a habitat appropriate for juvenile survivorship. The time required for development from egg to settled juvenile is strongly dependent on the mode of development. Thus in the following section, we examine developmental mode as a guide to understanding the duration of development in opisthobranchs. Since direct

Table 2. Settlement requirements of opisthobranchs with lecithotrophic larvae.

Species	Adult Food	Settlement Requirement	Reference
Nudibranchia			
Doridacea			
Adalaria proxima (Alder and Hancock)	*Electra pilosa* and other encrusting Bryozoa	*Electra pilosa*	Thompson (1958)[2]
Discodoris erythraeensis Vayssiere	fine algae and diatoms	surface	Gohar and Aboul-Ela (1959)[2]
Hoplodoris nodulosa (Angas)	sponges	surface	Rose (1983)
Aeolidiacea			
Eolidina mannarensis Rao	probably hydroids	surface	Rao and Alagarswami (1960)[2]
Eubranchus exiguus (Alder and Hancock)	*Kirchenpaueria pinnata* (Linnaeus) (Hydrozoa)	same[1]	Tardy (1962)[2]
E. farrani (Alder and Hancock)	*Aglaophenia pluma* (Linnaeus) and other hydroids	*Obelia geniculata* (Linnaeus)	Todd (1981)
Cuthona adyarensis Rao	*Bimeria* sp. and *Laomedea* sp. (Hydrozoa)	algae, etc.	Rao (1961)[2]
Phestilla sibogae Bergh	*Porites* spp. (Scleractinia)	same	Hadfield (1977)[2]
Tenellia pallida (Nordmann)	*Laomedea loveni* (Allman) and other hydroids	surface	Rasmussen (1944)[2] Eyster (1979)[2]
Dendronotacea			
Tritonia hombergi Cuvier	*Alcyonium digitatum* (Linnaeus)	same	Thompson (1962)[2]
Sacoglossa			
Berthelinia caribbea (Edmunds)	*Caulerpa verticillata* (Agardh)	same	Grahame (1969)[2]
B. limax Kawaguti and Baba	*C. okamurai* (Webber-Van Basse)	?	Yamasu (1969)[2]
Notaspidea			
Berthellina citrina (Rüppell and Leuckart)	probably ascidians	surface	Gohar and Aboul-Ela (1957)[2]

[1] settlement substratum is the same as adult food; [2] cited in Hadfield and Switzer-Dunlap, 1984.

developers place their juveniles directly into a habitat that the previous generation had already found to be salubrious, we conclude by looking to them to understand one of the primary questions of this essay: "When do larvae metamorphose?"

EGG SIZE AND DEVELOPMENTAL MODE

It has been traditional when comparing the three typical developmental modes of opisthobranchs or other marine invertebrates, pelagic-planktotrophic, pelagic-lecithotrophic and direct, to assume that they are three different means to the same end. In its simplest definition, that end is a metamorphosed juvenile in a habitat suitable for growth, survival and reproduction, and the major difference in the modes of development is the amount of energy packed into each ovum. This traditional view usually invokes "pie arguments." The components of these arguments are (1) across species there is a set amount or proportion of energy available for reproduction (= the pie) and (2) the number of offspring produced at birth is a function of how large each ovum is made (= the number of slices into which the pie is cut). When applied to larval biology, the pie arguments predict that, in general, small eggs result in small larvae which must feed in the plankton and grow to a size equal to that achieved at birth when the pie is sliced into fewer but larger pieces as in lecithotrophic and direct development. That is to say, all modes of development should produce settled juveniles of about the same size (e.g. Strathmann, 1978a, 1985).

We can now ask, is the prediction of uniform settling sizes across developmental modes valid for opisthobranchs? To answer this question we must examine a large amount of data that will allow us to compare egg sizes with juvenile sizes across developmental modes. The first step is to look at the distribution of egg sizes among opisthobranchs of different developmental modes to determine if egg size is smaller among species with planktotrophic development than among those with lecithotrophic-pelagic and direct development. Average egg diameters for pelagic-planktotrophic, pelagic-lecithotrophic and direct developers are 84 μm, 143 μm, and 200 μm, respectively. The differences are significant for planktotrophic eggs when compared to either of the other two modes (planktotrophic vs. lecithotrophic, $t = 8.355$, $P < 0.001$; planktotrophic vs. direct, $t = 9.171$, $P < 0.001$), and for the mean size of lecithotrophic-pelagic eggs compared to that of direct developers (t = 3.971, P < 0.001).

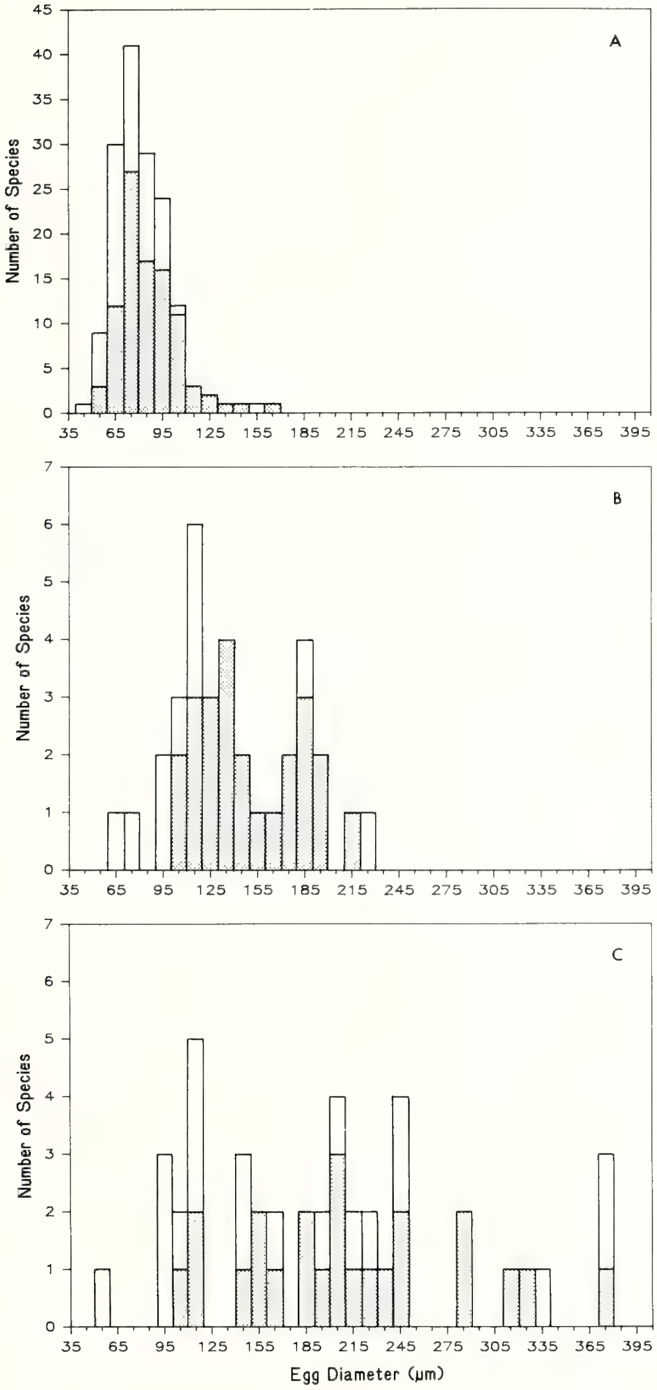

Fig. 1. Egg-size distribution in Opisthobranchia. **A.** Species with planktotrophic larval development. Hatched bars, Nudibranchia (n = 94); open bars, all other orders (n = 61). **B.** Species with lecithotrophic larval development. Hatched bars, Nudibranchia (n = 24); open bars, all other orders (n = 10). **C.** Species with direct development. Hatched bars, Nudibranchia (n = 23); open bars, all other orders (n = 20). (Note different vertical scales.)

Figure 1A displays egg-size distributions among opisthobranchs with planktotrophic larvae. It should be noted, (1) that the majority of species fall into a rather wide range of 45 to 130 μm diameter ova, (2) that the modal size, about 75 μm, is set by the most abundantly measured group, the Nudibranchia, and (3) that the eggs of Sacoglossa tend to be smaller (see Fig. 7).

The distribution of egg diameters in opisthobranch species with pelagic-lecithotrophic development is displayed in figure 1B. It is clear that the range of sizes is larger than for planktotrophic species; egg diameters fall between one hundred and two hundred microns. Again, it is notable that sacoglossans achieve lecithotrophy at smaller egg diameters (mean = 97 μm; n = 9), as previously noted by Clark and Jensen (1981).

Finally, the ova of species with direct development clearly achieve the largest sizes of all, with a range of diameters extending from 120 to 380 microns (Fig. 1C). These ova broadly overlap the sizes of planktic-lecithotrophs and extend to much larger sizes. In the direct developers with

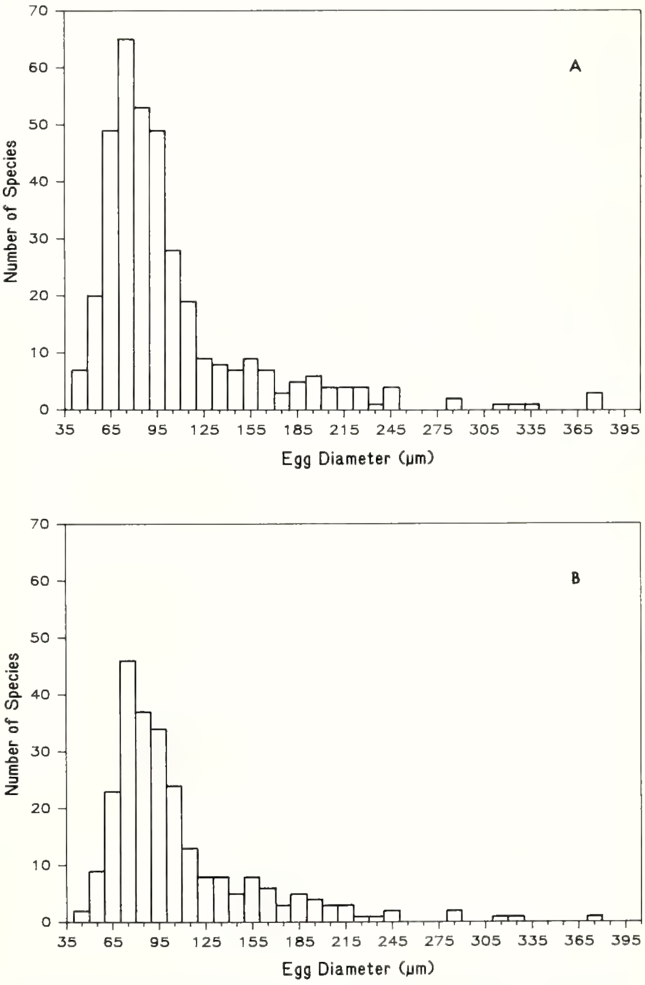

Fig. 2. A. Egg-size distribution in all Opisthobranchia (n = 369). **B.** Egg-size distribution in the Nudibranchia (n = 250).

smaller eggs, the clarity of mode is weakest. Many of these metamorphose at about the time of hatching, and some are even mixed, with some larvae metamorphosing in the egg jelly and others after a brief swim. Evolutionarily, these might be construed as species in transition from indirect to direct development.

We next examine the relative distributions of egg sizes among opisthobranchs. In figure 2A the frequency distribution of egg diameters across all opisthobranchs is plotted. It can be seen that (1) the range is wide, 40-380 μm, but (2) most ova fall into the narrow range of 60-110 μm, and (3) the basically unimodal distribution (with the mode about 75 μm) is skewed, with a long "tail" stretching out to the right. The same trends hold for successively smaller taxonomic units; similar data are plotted for the order Nudibranchia in figure 2B, for the nudibranch suborders Doridacea and Aeolidacea in figures 3 and 4, and for the families Dorididae and Chromodorididae in figures 5 and 6. Sacoglossa (Fig. 7) show a trend to smaller ova; these data are dominated by measurements made by Clark and co-workers on the Florida-Caribbean fauna, and it would be interesting to know if sacoglossans produce similarly small ova throughout world seas. The relatively small egg diameters seen in the modal size classes of all groups are strongly indicative of the dominance of the feeding larva in opisthobranch development (see below).

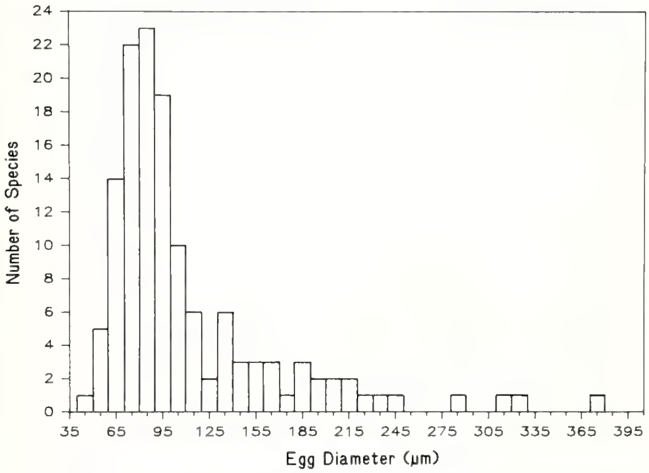

Fig. 3. Egg-size distribution in the nudibranch suborder Doridacea (n = 134).

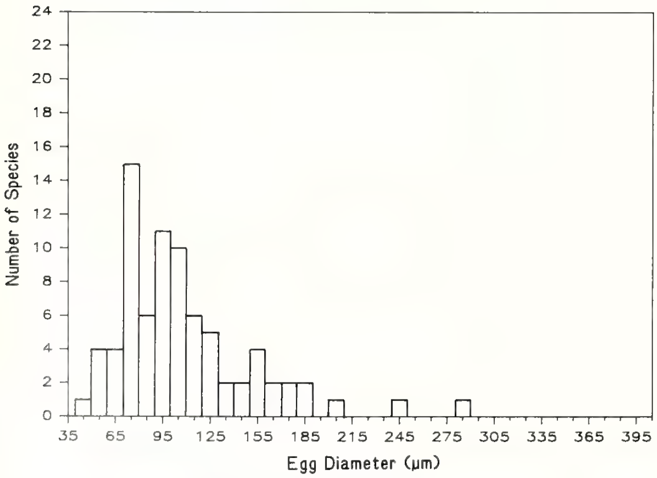

Fig. 4. Egg-size distribution in the nudibranch suborder Aeolidacea (n = 79).

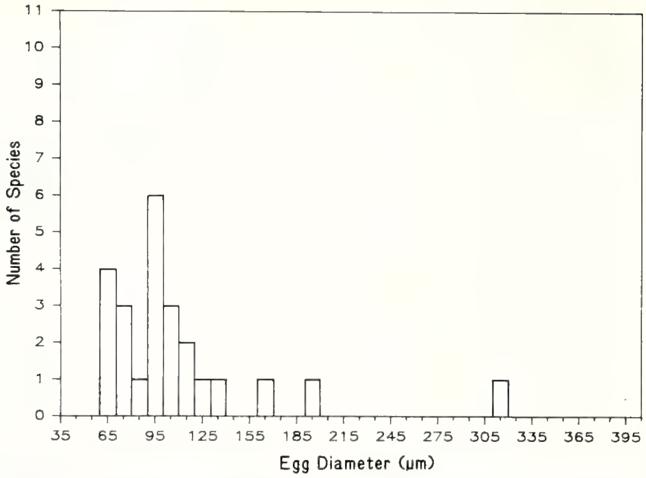

Fig. 5. Egg-size distribution in the nudibranch family Dorididae (n = 24).

Table 3 summarizes information gleaned from the literature on the numbers of species with different developmental modes in most opisthobranch orders. Species whose egg diameters were presented in the literature, but whose developmental modes were not stated, are included as an extra column. While most, if not all, of these probably have pelagic-planktotrophic development, they are not included in that category due to uncertainty. Judging strictly from the designated data, about 67% of all species studied have planktotrophic larvae, with the lecithotrophic-larval and direct modes accounting for about equal portions of the remainder. If, however, the uncertain species (column 5) are assumed

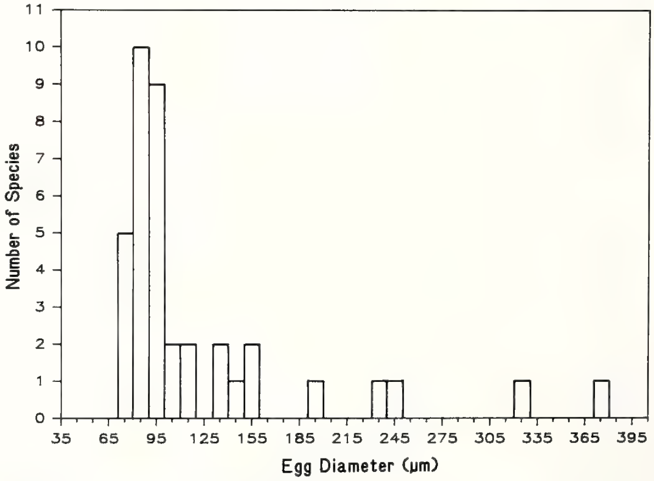

Fig. 6. Egg-size distribution in the nudibranch family Chromodorididae (n = 38).

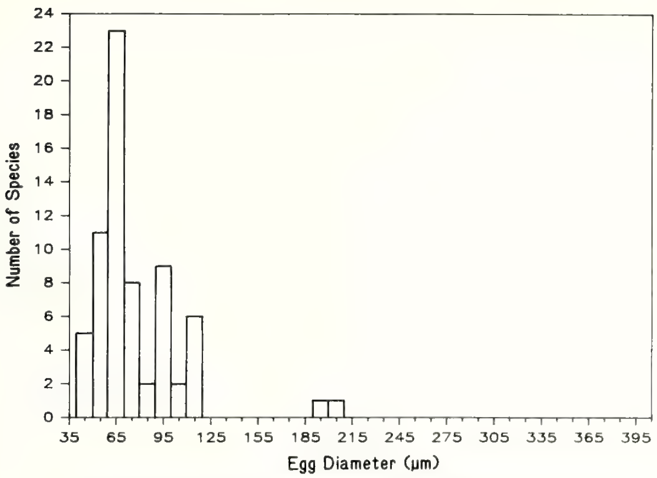

Fig. 7. Egg-size distribution in the order Sacoglossa (n = 68).

to have feeding larvae, the percentage of this type jumps to about 80%. Certainly this mode is by far the most abundant among opisthobranchs, a generalization that appears to hold for each of the major orders. From the data summarized in figures 1-7 and Table 3, we conclude that (1) egg size clearly distinguishes species with feeding larvae from those with non-feeding developmental modes (lecithotrophic-pelagic and direct) and (2) most opisthobranchs produce small eggs that develop into planktotrophic larvae.

Table 3. Developmental patterns in opisthobranchs.

Order	No. Spp. w/Plankto-trophic Dev.	No. Spp. w/Lecitho-trophic Dev.	No. Spp. w/ Direct Dev.	Egg Diameter only
Nudibranchia	100 (66%)	27 (18%)	24 (16%)	109
Cephalaspidea	16 (70%)	0	7 (30%)	1
Sacoglossa	31 (63%)	8 (16%)	10 (20%)	20
Anaspidea	17 (89%)	0	2 (11%)	0
Notaspidea	0	2	0	4
"Pteropods"	4 (67%)	0	2 (33%)	3
TOTAL	168 (67%)	37 (15%)	45 (18%)	[137]

IS THE TIMING OF METAMORPHOSIS SIZE DEPENDENT?

Egg size is a relatively good predictor of hatching shell size in opisthobranchs (Fig. 8): the larger the egg, the larger the shell size at hatching. Figure 9 shows that the generalization is quite sound for Nudibranchia alone and an additional important point. Shells of Type II (egg-shaped, inflated larval shells that do not grow during larval development) are much larger than Type I shells (coiled shells which do grow during development) arising from eggs of the same size (opisthobranch larval shell types are discussed by Thompson, 1961). This is probably related to the fact that space for body growth is included inside Type II shells, while it can be provided only by incremental growth in Type I shells. It can be further concluded from figure 10 that the relationship between egg size and hatching shell size is consistent even among smaller opisthobranch taxa (the nudibranch superfamily Doridacea and the family Chromodorididae). Due to the fact that a larval shell does not appear during the ontogeny of opisthobranchs with ametamorphic direct development, these opisthobranchs add nothing to understanding the egg-size:shell-size relationship.

If the hypothesis is valid that settlement is optimized at about the same size among related species, then predictions relating egg size (the equivalent of hatching size; Figs. 8-10) to larval period should hold. Because the amount of growth during the pelagic period of planktotrophic species is positively related to the duration of the pelagic period (see Hadfield and Switzer-Dunalp, 1984: Fig. 39), the duration of the pelagic period should correlate negatively with egg diameter; it can be seen from data in figure 11 that it does not. In fact, there is no clear relationship between hatching size and settling size, a point illustrated in figure 12.

Additionally, if there was an optimal settling size for species with lecithotrophic development, one would expect that all eggs producing lecithotrophic larvae would be of a similar size, which they clearly are not (Fig. 1B, 11), even within restricted taxonomic groups. Egg diameters range from under 100 µm to over 200 µm for lecithotrophic nudibranchs (n = 24), from 110 to 185 µm for lecithotrophic aeolidaceans (n = 15), and from 69 to 120 µm for lecithotrophic members of the order Sacoglossa (n = 8). It is possible that within highly restricted taxa such as families or genera, trends toward more uniform settling sizes may occur, but this is not obvious from currently available data.

Can we predict the mode of development of an opisthobranch species by examining characteristics of its biology other than egg diameter? Using the pie arguments, the most usual approach has been to attempt predictions based on adult energetics. The assumption, as stated previously, is that the energy available for reproduction will be a constant amount or proportion as one compares across species with different developmental modes. This has not turned out to be true (see Strathmann, 1985, for a discussion covering all types of invertebrates). Chia (1971), studying three sympatric sacoglossans with differing developmental modes, found that the amount of egg protoplasm produced differed greatly among the species. A species with planktotrophic larvae [*Limapontia capitata* (Müller)] produced nearly three times as much "egg protoplasm" as a directly developing species of about the same animal size (*Acteonia cocksi* Alder and Hancock). Todd (1979) compared two sympatric nudibranchs, one with planktotrophic and the other lecithotrophic pelagic development and found the caloric investment in ova to be greater in the lecithotrophic species, but the relative reproductive effort (dry weight of spawn divided by body dry weight) to be greater in the planktotrophic species. Sarver (1978) conducted experimental studies of reproductive effort (RE) in the anaspidean *Aplysia juliana* Quoy and Gaimard and found that RE varied over the lifespan of individuals and as a result of the amount of food eaten. These shifts were seen whether RE was measured as the

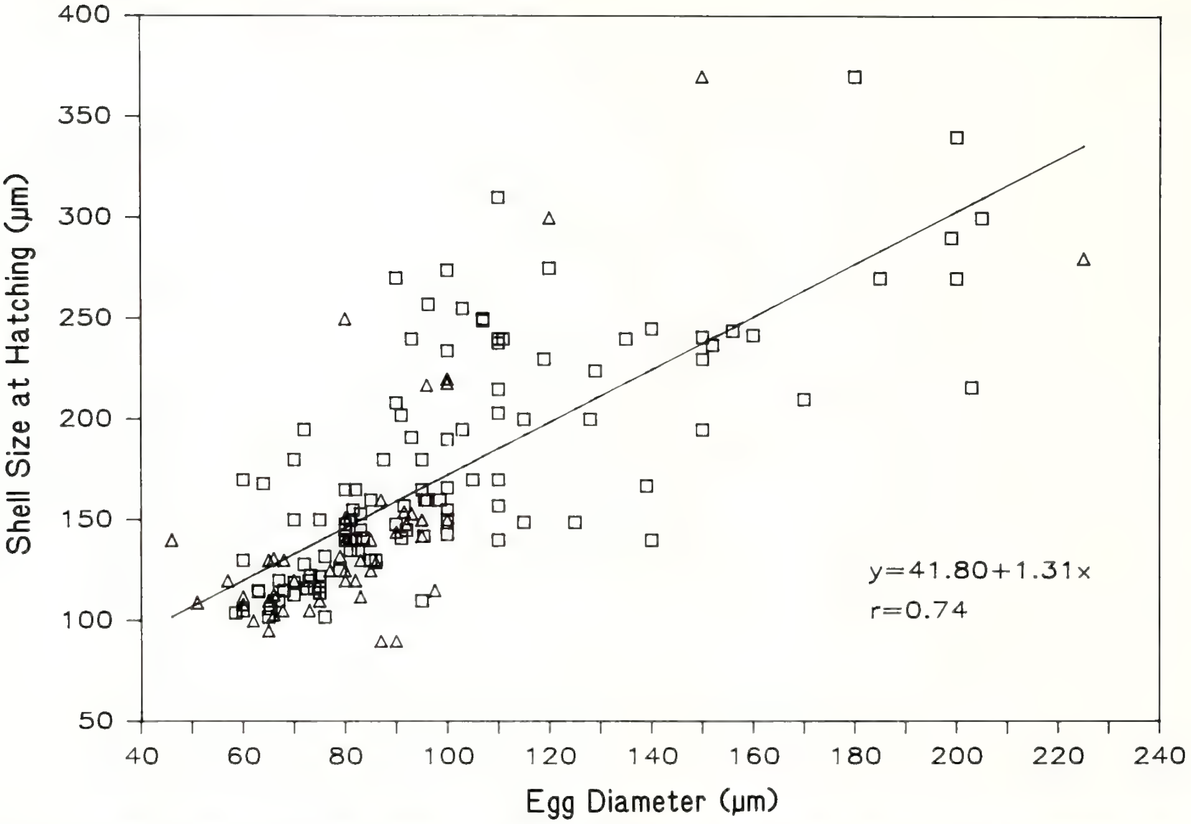

Fig. 8. Larval-shell length at hatching vs. egg diameter. □, Nudibranchia (n = 113); △, all other orders (n = 53). The cephalaspidean *Philine gibba* Strebel, egg diameter 379 µm, hatching size 375 µm, is not included.

percent of maximum body weight represented by the weight of all spawn produced during life, or as total calories spawned expressed as a percent of total calories ingested. Reproductive effort measured as weight was 135% for animals on *ad libitum* ration and about half that if provided with only three-quarters of the *ad libitum* amount. Expressed as calories, RE was 10.69 for *ad lib* ration and 7.25 for 75% ration. Because animals found in the field never achieved the size of *A. juliana* reared in the laboratory with an *ad libitum* food supply, Sarver concluded that the food regime of this animal is restrictive and that RE *in the field* must vary in time and space. It thus appears that there are no generalizations to be drawn relating reproductive energetics to developmental mode that can apply throughout the Opisthobranchia, and RE is not a useful predictor of developmental mode.

The absence of a correlation between egg size (thus hatching size) and settlement size and the lack of usefulness of reproductive effort in predicting developmental mode indicate that there are flaws in the original assumptions of the pie arguments, at least in application to most opisthobranchs. In addition to the absence of consistency in reproductive effort across or within developmental modes, it appears that another basic problem lies in the prediction that benthic juveniles resulting from all modes should be about the same size, at least within restricted taxa or ecological types (for example sponge feeders). We showed above that settling larval *shell* sizes differed among opisthobranchs with the same and different developmental modes, and we next examine the assumption that different modes of reproduction produce similarly sized benthic juveniles (i.e. shortly after metamorphosis). Here shell measurement is discarded except for groups like cephalaspideans where it could be a good measure of juvenile size. Examing juvenile size rather than shell size seems particularly important for the nudibranchs where the two different shell types have such different relationships with egg diameters (Fig. 9), and because all nudibranchs (which are the source of most data) and most sacoglossans shed their larval shells at metamorphosis, making shell measurements poor approximations of the size of newly metamorphosed juveniles.

The data presented in figure 13 reveal some rather surprising and, to us, not intuitive conclusions. First, as previously shown, planktotrophic larvae all arise from small eggs, with essentially no overlap with the other two modes of development. Secondly, although lecithotrophic larvae arise from larger eggs, there is a limit to size of the juvenile that results from pelagic development that is common to both pelagic modes; the limiting size is a juvenile about 500 µm long. Third, while there is a broad overlap of egg sizes between pelagic-lecithotrophic and direct developers, only some direct developers "escape" the juvenile size limitation of ~500 µm to produce very large juveniles, some of them up to a millimeter long. Most of the distribution of juvenile sizes among direct developers can be explained by the two patterns of development known in this group: metamorphic-direct developers (a shelled, veliger stage occurs within the egg mass) and ametamorphic-direct developers (a shell and most other vestiges of the veliger are lacking in their ontogeny) (see Bonar, 1978, for a discussion of these two modes). The ametamorphic direct developers are indicated by filled triangles in figure 13; resulting juveniles are clearly larger. These can be considered the most evolved in the direction of direct development. We conclude that the presence of a larval shell sets a maximum size limit on opisthobranch juveniles, a limit that doesn't exist, at least at such a small size, among prosobranchs.

The great spread in juvenile sizes and the apparent relationship between juvenile size and developmental mode might be due to mis-interpretation of existing data since different types of opisthobranchs have different length-to-weight ratios; only good weight measurements of newly metamorphosed juveniles would resolve this problem. On the other hand, juvenile length could provide a valid measure of size as it relates to predator avoidance. For some species, factors unrelated to selection for juvenile size might relate developmental mode to different aspects of their biology; one is adult size (Menge, 1975; Strathmann and Strathmann, 1982). Arguments relating adult size to developmental mode have been devoted to brooding, a habit unknown for opisthobranchs (with a possible exception cited by Rose and Hoegh-Guldberg, 1982). The arguments assume that small animals, having an absolute (and small) limit on the amount of energy available for reproduction must take the "safer" path of direct development, by-passing the plankton as a source of nutrition and dispersal to avoid it as a great source of developmental mortality. Table 4 lists directly developing species for which we could find data on adult lengths as well as juvenile lengths. It is clear that both large and small species produce large eggs that develop directly into hatching benthic juvenile stages. Still, reduction in adult size may have driven selection for direct development in some species.

Another possibility, alluded to above, is that certain ecological conditions could predicate different "best sizes" after metamorphosis. This hypothesis defies clear testing, but at least among specialized feeding groups (e.g. sponge feeders; hydrozoan feeders; bryozoan feeders) no generalizations about optimal juvenile sizes emerge from our data set. A wide range of juvenile sizes occur among all such groups, as they do among taxa which tend to have similar dietary habits (e.g. Sacoglossa).

We propose the following hypothesis to explain the observations delineated above. Post-settlement mortality is size dependent; the larger the juvenile size, the greater the freedom from predation by one or more common groups of micro-carnivores (mainly small worms and crustaceans; e.g. Highsmith, 1982). Juvenile mortality is least among opisthobranch species with ametamorphic-direct development because the hatching juveniles of these species are suf-

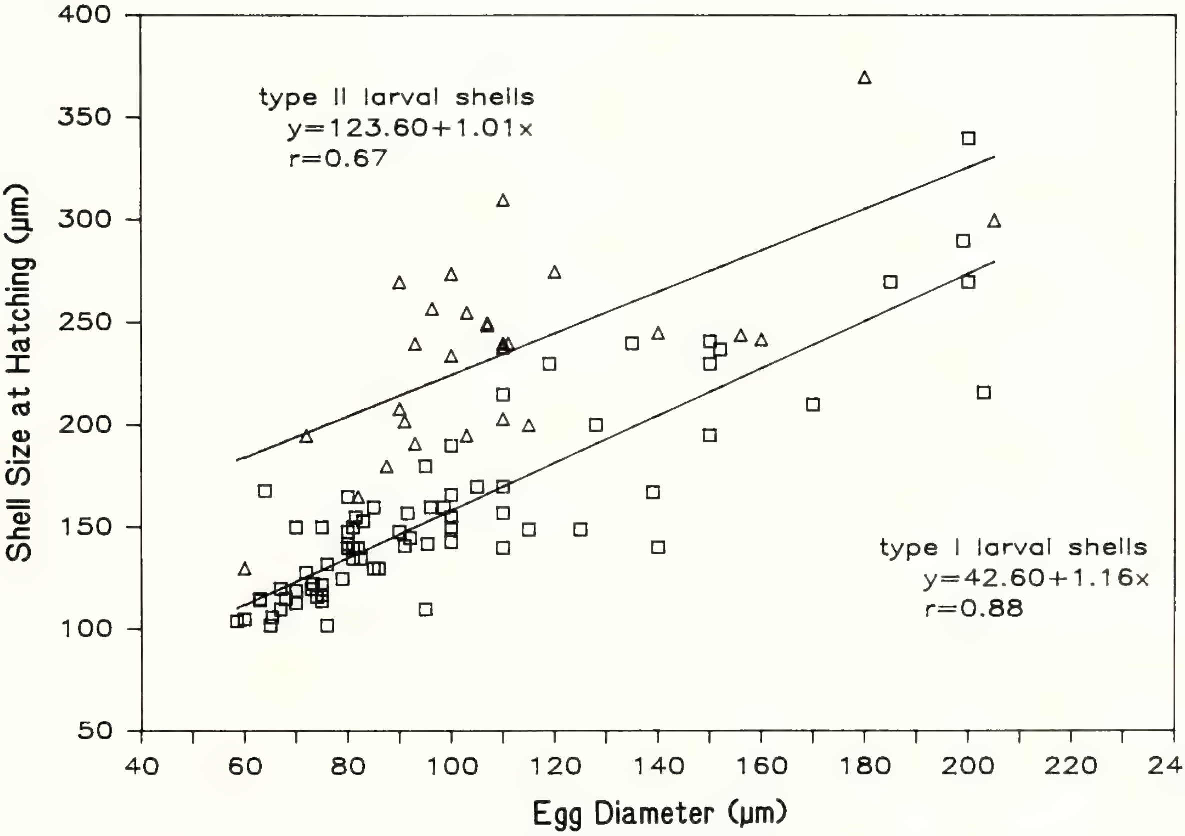

Fig. 9. Larval-shell length at hatching vs. egg diameter in the Nudibranchia. □,Type I larval shells (n = 75); △,Type II larval shells (n = 28).

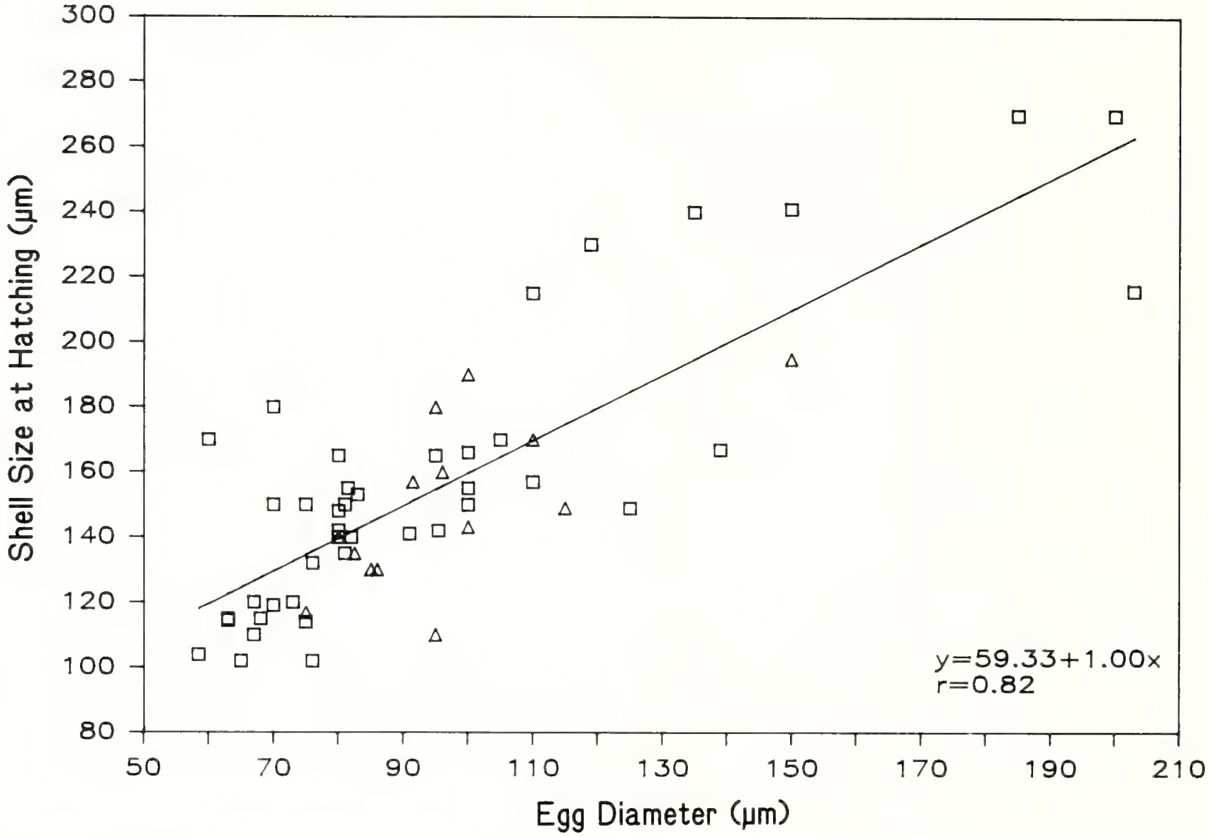

Fig. 10. Larval-shell length at hatching vs. egg diameter in the nudibranch suborder Doridacea (n = 57). △, family Chromodorididae (n = 14).

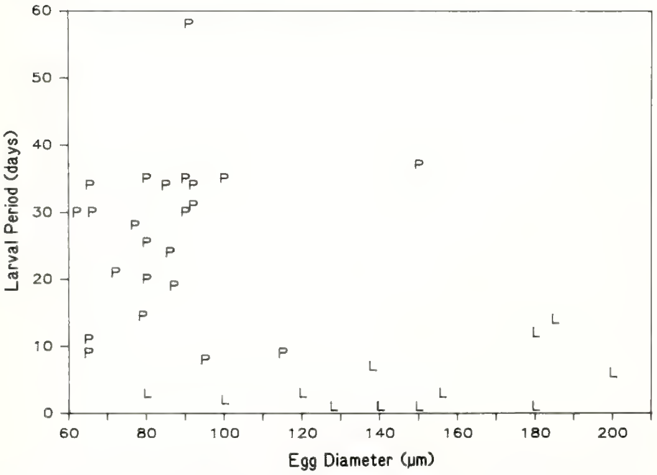

Fig. 11. Larval duration vs. egg diameter in the Opisthobranchia. P, species with planktotrophic development (n = 23); L, species with lecithotrophic development (n = 13).

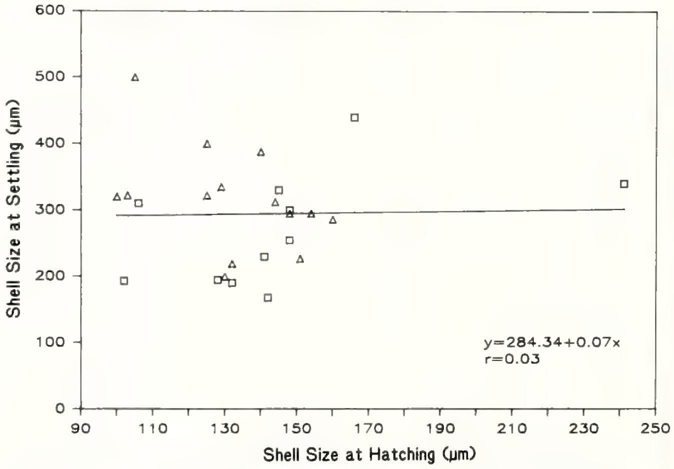

Fig. 12. Larval-shell length at settlement vs. larval-shell length at hatching. □, Nudibranchia (n = 11); △, all other orders (n = 14). (Only nudibranchs with Type I shells are included).

ficiently large and well developed to avoid (by size, behavior or other factors) most micro-carnivores. The large number of larvae produced by species with pelagic-planktotrophic development are necessary to assure adult replacement after extensive mortality both in the plankton and *in early benthic stages.* Pelagic-lecithotrophic larvae, because of their brief planktic existence, suffer less mortality in the plankton, but because their metamorphic size is small, must still be produced in sufficiently large numbers to offset high early juvenile mortality. Data to support this hypothesis are scant. Only the field studies of Sarver (1979) on the sea hare *Aplysia juliana* have documented early post-settlement mortality for an opisthobranch. Sarver calculated mortality rates in excess of 16% per day for newly settled *A. juliana.* But individuals of this species, like most sea hares, produce hundreds of millions of offspring; its success is indicated by its distribution throughout tropical and subtropical seas of the world, and even into temperate regions such as Japan. This hypothesis predicts a great reduction in numbers of offspring in the shift from metamorphic to ametamorphic direct development. However, life-time fecundity data are not sufficiently abundant to test this prediction.

What determines the developmental mode of any individual opisthobranch species? Assuredly, there is no single answer. Given the preponderance of species with planktotrophic larvae (more than 70% of all opisthobranchs), we assume that this is the primitive mode for the group, an assumption strengthened by the unlikelihood of evolution from direct development to larviparous development (Strathmann, 1978b). Thus the evolutionary direction will be toward lecithotrophic-planktic development and from there to direct development. The most evolved forms, in terms of this life history adaptation, will be those with ametamorphic direct development. It is probable that the selective pressures leading away from planktotrophic development have not been the same across all opisthobranch species.

Selection can occur at any life-history stage. If mortality is too great in the pelagic phase, that phase can be reduced or eliminated. For example, it is possible that direct development evolved in some species in response to a brief and unreliable polar phytoplankton season, as suggested by Thorson (1950). Intense predation on early juveniles could have selected for increased size, which we have shown to be limited by pelagic development. Thus direct development evolves. Finally, any process that restricts adult size could also limit fecundity and thus influence the evolution of lecithotrophic or direct development. In some cases, a predatory opisthobranch could have adapted to a relatively short-lived prey (e.g. some hydrozoans) by itself becoming short-lived in order to grow to maturity and reproduce before the prey is exhausted. The adaptation will almost certainly include a considerable reduction in predator size, and thus, fecundity. Under these conditions, larger, lecithotrophic eggs will be favored for reasons discussed above. If prey are not too patchy, pelagic larvae could be dispensable, and the reduced fecundity related to small size will be further compensated by the production of still larger, directly developed offspring with a concomitant reduction in both larval and juvenile mortality. In other cases, competition could have restricted the growth of a species and thus reduced its reproductive output to the point where it could not successively replace itself via a larviparous mode (an argument made

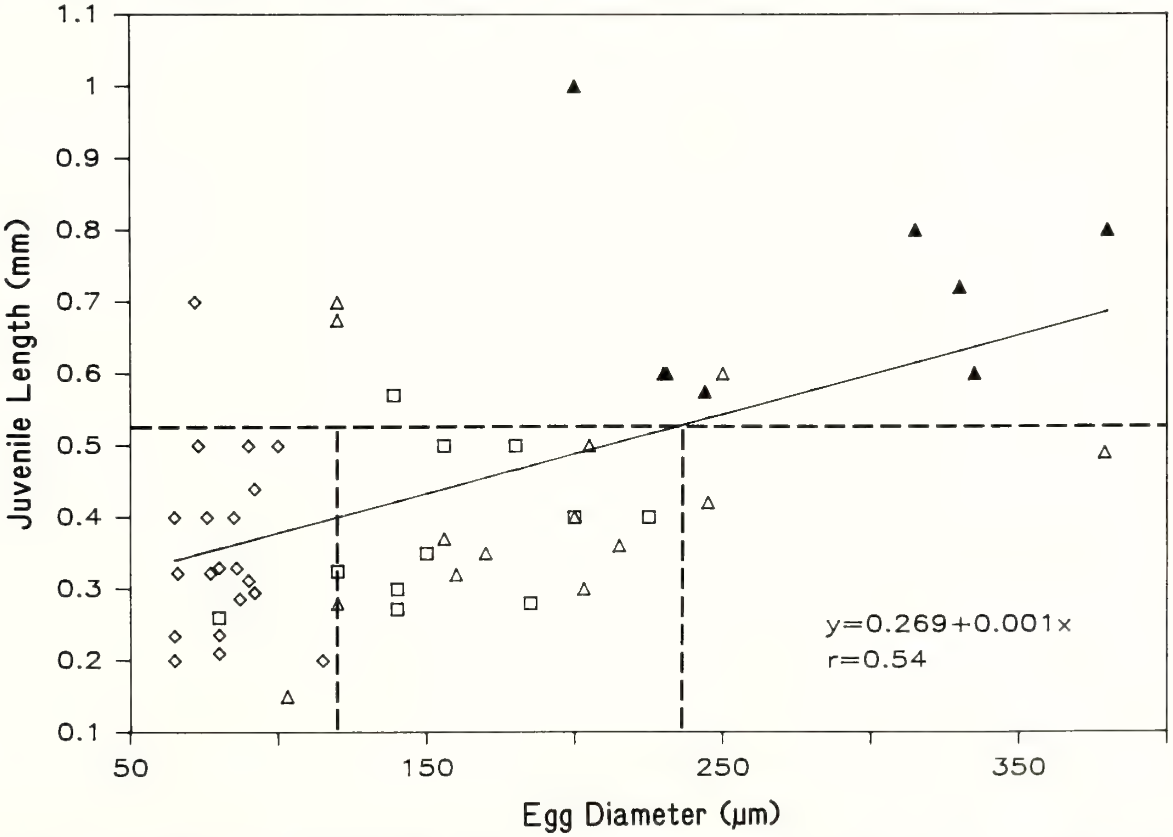

Fig. 13. Length of post-metamorphic juveniles vs. egg diameter. ◇, species with planktotrophic larvae (n = 21); □, species with lecithotrophic larvae (n = 11); △, species with metamorphic direct development (n = 14); ▲, species with ametamorhpic direct development (n = 8). The vertical dashed lines emphasize the egg-size limits of species with the planktotrophic and lecithotrophic development. The horizontal dashed line indicates the upper limit of juvenile length for most species which have a larval shell in their development.

Table 4. Egg size, juvenile size and adult size for directly developing opisthobranchs.

Species	Egg. Diam.	Juv. L.	Adult L.	Dev.[1]	Reference
Nudibranchia					
Trippa spongiosa (Kelaart)	200 µm	400 µm	55 mm	M	Gohar and Soliman (1967)[2]
Casella obsoleta (Rüppell and Leuckart)	315	800	46	A	Gohar and Soliman (1967)[2]
Cadlina laevis (Linnaeus)	380	800	32	A	Thompson (1967)[2]
Chromodoris loringi (Angas)	330	720	15	A	Thompson (1972)[2]
Hypselodoris bennetti (Angas)	231	600	30	A	Thompson (1972)[2]; Rose (1981)[2]
Glossodoris gracilis von Rapp	244	575	36	A	Gantès (1962)
Dendrodoris miniata (Alder and Hancock)	215	360	28	M	Thompson (1975); Rose (1981)[2]
Doriopsilla pharpa Marcus	203	300	25	M	Eyster and Stancyk (1981)[2]
Okadaia elegans Baba	230	600	<5	A	Baba (1937)[2]
Cuthona granosa (Schmekel)	120	280	11	M	Schmekel and Portmann (1982)
C. nana (Alder and Hancock)	160	320	28	M	Rivest (1978)[2]
C. pustulata (Alder and Hancock)	205	500	20	M	Roginskaya (1962)[2]
Tenellia pallida (Nordmann)	103	150	3	M	Eyster (1979)[2]
Dermatobranchus striatellus Baba	170	350	10	M	Hamatani (1967)[2]
Cephalaspidea					
Runcina ferruginea Kress	335	600	4	A	Kress (1977)[2]
R. setoensis Baba	250	600	<7	M	Baba and Hamatani (1959)[2]
Retusa obtusa (Montagu)	245	421	10	M	Smith (1967)[2]
Philine gibba Strebel	379	490	12	M	Seager (1979)[2]
Sacoglossa					
Acteonia cocksi Alder and Hancock	200	1000	6	A	Chia (1971)
Elysia timida Risso	120	700	12	M	Rahat (1976)[2]
Oxynoe azuropunctata Jensen	120	675	40	M	Jensen (1980)
Anaspidea					
Phyllaplysia taylori Dall	150	370	45	M	Bridges (1975)[2]

[1] Development; M = metamorphic; A = ametamorphic. [2] Cited in Hadfield and Switzer-Dunlap, 1984.

for starfish by Menge, 1975).

Are these suggested explanations for the occurrence of lecithotrophic or direct development "pie arguments"? No, in that there are no clear and predictable effects on settling size or reproductive investment per egg associated with the different developmental modes as predicted by the pie arguments. The advantage provided by a shift from planktotrophy to lecithotrophy is a decrease in larval mortality due to a shorter planktic period (see Fig. 11). A shift to direct development (especially ametamorphic direct development) provides a further advantage, that of reduced juvenile mortality due to larger juvenile size. Where the pie arguments fail for opisthobranchs is in explaining the large numbers of minute forms that succeed with planktotrophy and the large animals that have lecithotrophic or direct development. To further sort out these potential explanations critical information is needed on average lifespans, life-time fecundities, developmental modes, larval durations, and weights of newly metamorphosed juveniles for large numbers of species with an emphasis on closely related groups living in sympatry and separated across latitudinal clines.

CONCLUSIONS

The developmental (embryonic plus larval) period for any opisthobranch species is undoubtedly under strong genetic constraints. These determine egg size (and thus hatching size), larval shell type (and thus larval growth pattern), growth rate (which is further modulated by temperature and food abundance), and settling size (which seems to be limited at a high phylogenetic level for species with a genuine larva). These factors are all important in determining the age at which larvae become metamorphically competent. For most opisthobranchs the precompetent larval period does not greatly exceed one month.

Once a larva is metamorphically competent, the duration of the larval period is determined by the availability of appropriate settlement substrata. Opisthobranch veligers (both planktotrophic and lecithotrophic) have been shown experimentally to be able to extend their larval periods considerably in the absence of settlement inducing substrata (Kempf, 1981; Paige, 1986). Facultative feeding increases the capacity for prolonged planktic existence in lecithotrophic species (Kempf and Hadfield, 1985).

Competent larvae of opisthobranchs settle in response to a variety of settlement cues ranging from specific soluble or adsorbed chemicals to common marine bacteria and fungal films. Species with highly specific food requirements generally settle in response to chemical cues arising from the food substance. Species with less specific food requirements settle in response to more general environmental characteristics associated with an appropriate habitat or food item.

If there is a "strategy" for reproductive mode in most species, it is to maintain recruitment potential as high as possible throughout the broadest appropriate time of the year (i.e. when food is available) (Hadfield and Switzer-Dunlap,

Table 5. Sources of data for opisthobranchs (see also Hadfield and Switzer-Dunlap, 1984).

Species	Data on: Egg Size	Embryonic Develop.	Larval Develop.	Hatching Size	Settling Size	References
Nudibranchia						
Acanthodoris brunnea MacFarland	X	X		X		Strathmann, pers. comm.**
A. hudsoni MacFarland	X	X				Hurst, 1967; Strathmann, pers. comm.
A. nanaimoensis O'Donoghue		X		X		Hurst, 1967
A. pilosa (Müller)*	X	X	X	X		Strathmann, pers. comm.
Adalaria sp.	X	X		X		Goddard, 1984
Aegires albopunctatus MacFarland	X					Strathmann, pers. comm.
A. punctilucens (d'Orbigny)	X	X				Schmekel and Portmann, 1982
A. sublaevis Odhner	X	X				Schmekel and Portmann, 1982
Aldisa binotata Pruvot-Fol	X					Millen and Gosliner, 1985
A. cooperi Robilliard and Baba	X	X				Millen and Gosliner, 1985
A. pikokai Bertsch and Johnson	X					Millen and Gosliner, 1985
A. sanguinea Cooper	X					Millen and Gosliner, 1985
A. tara Millen	X	X	X			Millen and Gosliner, 1985
Ancula pacifica MacFarland	X	X		X		Goddard, 1984
Anisodoris nobilis MacFarland	X	X		X		Goddard, 1984
Antonietta luteorufa Schmekel	X	X				Schmekel and Portmann, 1982
Archidoris odhneri MacFarland		X		X		Hurst, 1967
A. pseudoargus (von Rapp)*	X	X	X	X	X	Schmekel and Portmann, 1982; Todd and Havenhand, 1985
Armina californica (Cooper)	X	X		X		Hurst, 1967; Strathmann, pers. comm.
A. maculata Rafinesque	X					Schmekel and Portmann, 1982
Babaina sp.	X	X	X			Boucher, 1983
Cadlina modesta MacFarland	X	X		X		Goddard, 1984
Calma glaucoides (Alder and Hancock)	X					Schmekel and Portmann, 1982
Calmella cavolini (Verany)	X					Schmekel and Portmann, 1982
Catriona gymnota (Couthouy)	X	X				Schmekel and Portmann, 1982
C. maua Marcus and Marcus		X				Schmekel and Portmann, 1982
Chromodoris sp. E6	X	X		X		Boucher, 1983
Chromodoris sp. E57	X	X		X		Boucher, 1983
C. albopunctatus (Garrett)	X	X	X	X		Boucher, 1983
C. inornata Pease	X	X	X	X		Boucher, 1983
C. krohni (Verany)	X					Schmekel and Portmann, 1982
C. luteopunctata (Gantés)				X		Edmunds, 1982
C. tryoni (Garrrett)	X	X	X	X		Boucher, 1983
Cratena peregrina (Gmelin)	X	X				Schmekel and Portmann, 1982
Crimora coneja Marcus	X	X		X		Goddard, 1984
C. papillata Alder and Hancock	X	X				Schmekel and Portmann, 1982
Cumanotus beaumonti (Eliot)				X		Hurst, 1967
Cuthona albocrusta MacFarland		X		X		Hurst, 1967
C. albopunctata (Schmekel)	X	X				Schmekel and Portmann, 1982
C. caerulea (Montagu)	X	X				Schmekel and Portmann, 1982
C. cocoachroma (Williams and Gosliner)	X	X		X		Goddard, 1984
C. columbiana (O'Donoghue)	X	X		X		Goddard, 1984
C. divae (Marcus)	X	X		X		Goddard, 1984
C. genovae (O'Donoghue)	X	X				Schmekel and Portmann, 1982
C. granosa (Schmekel)*	X	X	X			Schmekel and Portmann, 1982
C. ilonae (Schmekel)	X	X				Schmekel and Portmann, 1982
C. ministriata (Schmekel)	X	X				Schmekel and Portmann, 1982
C. ocellata (Schmekel)	X					Schmekel and Portmann, 1982
C. poritophages Rudman		X	X			Rudman, 1979
C. pustulata (Alder and Hancock)*	X	X	X			Gosliner and Millen, 1984
Dendrodoris krebsii (Mörch)*	X		X			DeFreese and Clark, 1983

(continued)

Table 5. (continued)

	Data on:					
Species	Egg Size	Embryonic Develop.	Larval Develop.	Hatching Size	Settling Size	References
D. nigra Stimpson*	X	X	X	X		Rose, 1985
Dendronotus diversicolor Robilliard	X	X				Robilliard, 1970; Strathmann, pers. comm.
D. frondosus (Ascanius)*	X	X	X	X		Williams, 1971
D. iris Cooper	X	X		X		Hurst, 1967; Strathmann, pers. comm.
Diaphana californica Dall	X	X		X		Goddard, 1984
Dicata odhneri Schmekel	X	X				Schmekel and Portmann, 1982
Dirona albolineata Cockrell and Eliot	X			X		Hurst, 1967; Strathmann, pers. comm.
D. aurantia Hurst		X		X		Hurst, 1967
Discodoris heathi MacFarland	X	X		X		Goddard, 1984
D. maculosa (Bergh)	X					Schmekel and Portmann, 1982
D. sandiegensis (Cooper)		X		X		Hurst, 1967; Strathmann, pers. comm.
Doris ocelligera (Bergh)	X	X				Schmekel and Portmann, 1982
Doto acuta Schmekel and Kress	X	X				Schmekel and Portmann, 1982
D. amyra Marcus	X	X		X		Goddard, 1984
D. coronata (Gmelin)*	X	X	X	X		Schmekel and Portmann, 1982
D. doerga Marcus and Marcus	X	X				Schmekel and Portmann, 1982
D. kya Marcus	X	X		X		Goddard, 1984
D. paulinae Trinchese	X	X				Schmekel and Portmann, 1982
D. rosea Trinchese		X				Schmekel and Portmann, 1982
Embletonia pulchra faurei (Alder and Hancock)	X	X				Schmekel and Portmann, 1982
Eubranchus exiguus (Alder and Hancock)*	X	X	X	X		Schmekel and Portmann, 1982
E. olivaceus (O'Donoghue)		X		X		Hurst, 1967
E. rustyus (Marcus)	X	X		X		Goddard, 1984
Facelina dubia Pruvot-Fol		X				Schmekel and Portmann, 1982
F. fusca Schmekel	X	X	X			Schmekel and Portmann, 1982
F. punctata (Alder and Hancock)	X					Schmekel and Portmann, 1982
Fiona pinnata (Eschscholtz)	X	X				Schmekel and Portmann, 1982
Flabellina affinis (Gmelin)		X				Schmekel and Portmann, 1982
F. fusca (O'Donoghue)				X		Hurst, 1967; Strathmann, pers. comm.
F. salmonacea (Couthouy)*	X	X	X			Kuzirian, 1979; Eyster, 1985
F. trilineata O'Donoghue	X	X		X		Bridges and Blake, 1972; Strathmann, pers. comm.
F. verrucosa (Sars)		X		X		Hurst, 1967; Strathmann, pers. comm.
Glossodoris bilineata Pruvot-Fol		X		X		Gantès, 1962
G. gracilis von Rapp	X	X				Gantès, 1962
G. luteopunctata Gantès		X		X		Gantès, 1962
Goniodoris castanea Alder and Hancock	X	X				Schmekel and Portmann, 1982
Gymnodoris sp.	X	X		X		Boucher, 1986
G. striata Eliot	X	X	X	X		Boucher, 1986
Hallaxa chani Gosliner and Williams	X	X		X		Goddard, 1984
Hancockia uncinata (Hesse)		X				Schmekel and Portmann, 1982
Hoplodoris nodulosa (Angas)*	X	X	X	X		Rose, 1983
Hypselodoris messinensis (von Ihering)	X					Schmekel and Portmann, 1982
Laila cockerelli MacFarland	X	X		X		Goddard, 1984
Limenandra nodosa Haefelfinger and Stamm	X	X				Schmekel and Portmann, 1982

(continued)

Table 5. (continued)

Species	Data on: Egg Size	Embryonic Develop.	Larval Develop.	Hatching Size	Settling Size	References
Melibe fimbriata Alder and Hancock	X	X	X			Thompson and Crampton, 1984
M. leonina (Gould)*	X	X	X	X	X	Bickell and Kempf, 1983
Miamira sinuata (van Hasselt)	X	X	X	X		Boucher, 1983
Onchidoris sp.	X	X		X		Goddard, 1984
O. muricata (Müller)*	X	X	X	X	X	Goddard, 1984; Todd and Havenhand, 1985
O. neapolitana (Delle Chiaje)		X				Schmekel and Portmann, 1982
Peltodoris atromaculata Bergh	X					Schmekel and Portmann, 1982
Phestilla sibogae Bergh*	X	X	X	X		Hadfield and Switzer-Dunlap, 1984
Phylliroe bucephala Péron and Lesueur	X	X				Schmekel and Portmann, 1982
Piseinotecus sphaeriferus (Schmekel)	X	X				Schmekel and Portmann, 1982
Platydoris scabra (Cuvier)	X	X	X	X		Soliman, 1978
Polycera quadrilineata (Müller)*	X	X	X	X		Schmekel and Portmann, 1982
P. zosterae O'Donoghue	X			X		Strathmann, pers. comm.
Polycerella emertoni Verrill	X	X				Schmekel and Portmann, 1982
Precuthona divae Marcus	X	X		X		Goddard, 1984
Pteraeolidia ianthina (Angas)*	X	X	X	X		Rose and Hoegh-Guldberg, 1982
Scyllaea pelagica Linnaeus	X		X			DeFreese and Clark, 1983
Sebradoris crosslandi (Eliot)	X	X	X	X		Soliman, 1980
Tergipes tergipes (Forskal)*	X					Schmekel and Portmann, 1982
Tethys fimbria Linnaeus	X					Schmekel and Portmann, 1982
Thecacera pennifera (Montagu)	X					DeFreese and Clark, 1983
Thordisa filix Pruvot-Fol	X	X				Schmekel and Portmann, 1982
Thorunna clitonata (Bergh)	X	X	X	X		Boucher, 1983
T. decussata (Risbec)	X	X	X	X		Boucher, 1983
T. norba (Marcus and Marcus)	X	X	X	X		Boucher, 1983
Trapania maculata Haefelfinger	X					Haefelfinger, 1960
Triopha catalinae (Cooper)	X	X		X		Strathmann, pers. comm.
Tritonia festiva (Stearns)	X	X		X		Goddard, 1984
Tritoniopsis cincta Pruvot-Fol		X				Schmekel and Portmann, 1982
Sacoglossa						
Aplysiopsis smithi (Marcus)	X	X		X		Goddard, 1984
Bosellia mimetica Trinchese*	X	X				Schmekel and Portmann, 1982
Caliphylla mediterranea Costa*	X	X				Schmekel and Portmann, 1982
Calliopaea bellula d'Orbigny		X				Schmekel and Portmann, 1982
Costasiella ocellifera (Simroth)	X					DeFreese and Clark, 1983
Cyerce cristallina (Trinchese)	X	X				Schmekel and Portmann, 1982
Elysia sp.	X		X			DeFreese and Clark, 1983
E. chlorotica (Gould)*	X	X		X		West, Harrigan and Pierce, 1984
E. hedgpethi (Marcus)*	X	X		X		Strathmann, pers. comm.
E. hopei (Marcus)	X	X	X	X		Thompson and Salghetti-Drioli, 1984
E. patina Marcus	X		X			DeFreese and Clark, 1983
E. subornata (Verrill)	X					DeFreese and Clark, 1983
E. tuca Marcus*	X		X			DeFreese and Clark, 1983
Ercolania funerea (Costa)	X	X				Schmekel and Portmann, 1982
E. fuscata (Gould)	X		X			DeFreese and Clark, 1983
Hermaea bifida (Montagu)	X		X			Schmekel and Portmann, 1982
Lobiger serradifalci (Calcara)		X				Schmekel and Portmann, 1982
Olea hansineensis Agersborg		X		X		Strathmann, pers. comm.
Placida cremoniana (Trinchese)		X				Schmekel and Portmann, 1982
P. viridis (Trinchese)*		X				Schmekel and Portmann, 1982
Stiliger fuscovittatus Lance				X		Strathmann, pers. comm.
Tridachia crispata Mörch*		X	X			DeFreese and Clark, 1983

(continued)

Table 5. (continued)

	Data on:					
Species	Egg Size	Embryonic Develop.	Larval Develop.	Hatching Size	Settling Size	References
Cephalaspidea						
Aglaja ocelligera (Bergh)		X	X	X		Hurst, 1967
Chelidonura sp.			X			DeFreese and Clark, 1983
Gastropteron pacificum Bergh		X				Hurst, 1967
Haminoea sp.		X	X			Strathmann, pers. comm.
H. antillarum (d'Orbigny)	X					DeFreese and Clark, 1983
H. vesicula (Gould)	X	X		X		Hurst, 1967; Strathmann, pers. comm.
Melanochlamys diomedea (Bergh)		X	X	X		Hurst, 1967
Anaspidea						
Phyllaplysia engeli Marcus*	X		X			DeFreese and Clark, 1983
Notaspidea						
Berthella californica (Dall)	X	X		X		Goddard, 1984

*Species that were previously listed in Hadfield and Switzer-Dunlap, 1984, for which new references are available.

**M. F. Strathmann, Friday Harbor Laboratories, University of Washington.

1984). Thus when short lived, sessile and rapidly growing foods (hydrozoans, bryozoans, algae) become available, larvae are available to take advantage of them. To accomplish this, most species are limited to smaller juveniles due to a not-understood limitation on the upper size of planktic opisthobranch veligers. The numbers of eggs (and thus larvae) produced must be sufficiently high to offset both larval mortality and increased juvenile mortality (relative to that of ametamorphically directly developing species). Species with direct development are far more limited in their spatial dispersal, but their large birth size imbues them with a greater likelihood of survival.

The puzzle remains as to why we often find all three developmental modes occurring among sympatric opisthobranchs, often even among family mates or congeners with the same or similar food requirements. Alas, shell-less opisthobranchs fossilize badly and for most we shall never know the place or time of their evolutionary divergence. However, we have no valid reason to assume that species currently found together evolved in sympatry or under the conditions in which they are now found. These limitations will always restrict our ability to construct predictive models for the pattern of reproduction of any opisthobranch species or for its larval longevity.

Data on opisthobranch larval settling size and on the allocation of energy to reproduction by adults do not support the predictions of "pie arguments", often suggested as an explanation for species-specific developmental mode. Settling sizes of larvae vary widely within and between planktotrophy, lecithotrophy and direct development. Energy allocated to reproduction by adults cannot be predicted from developmental mode in the few species for which data are available. In addition, pie argument predictions correlating egg size (or hatching size) with settling size or with larval duration are not supported by the data.

Given the poor value of most quantifiable life-history traits (egg size, reproductive effort, adult size, food type) in predicting developmental mode, we suggest that crucial selective pressures often occur during planktic larval phases, at the time of recruitment, and during early juvenile development.

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PHYLOGENETIC SYSTEMATICS OF THE NOTASPIDEA (OPISTHOBRANCHIA) WITH REAPPRAISAL OF FAMILIES AND GENERA

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ABSTRACT

Character states for 57 qualitative characters are described for the opisthobranch order Notaspidea and their distribution among Recent genera tabulated. Characters employed pertain to behavior, body form, mantle, shell, jaws, radula, comparative anatomy of the gut and reproductive system. Primitive and advanced conditions for each character are inferred on the basis of outgroup comparisons. Data from this matrix are used to construct a phylogenetic hypothesis by application of the Hennigian method and rule of parsimony. This phylogenetic cladogram is compared to an unweighted, computer-generated dendrogram. Data from these cladistic and phenetic analyses are employed in reappraising higher taxa of the order. Two suborders, three families, two subfamilies, two tribes and 11 genera are recognized. Characters defining each taxon are briefly ennumerated and examined to consider inter-relations; this consideration extends to reconsideration of synonymous genera.

Opisthobranch gastropods belonging to the order Notaspidea display considerable heterogeneity of body form yet all possess a bipinnate gill on the right side which lies longitudinally between the mantle and foot and is attached to the body for the greater part of its length. The significance of this (symplesiomorphic) side-gilled condition is that it is a necessary intermediate stage in the transition from the primitive, shelled "tectibranch" grade of opisthobranch body organization to the advanced "nudibranch" one as seen in Recent opisthobranchs belonging to the order Anthobranchia (= Doridacea). Indeed such a transitional series is seen in the gill/anal interrelations of modern deep-sea anthobranch nudibranchs belonging to the primitive genus *Bathydoris* (Evans, 1914; Minichev, 1970). Notaspideans are thus prime candidates as ancestors of anthobranch nudibranchs (Odhner, 1939; Ghiselin, 1966; Minichev, 1970; Faulkner and Ghiselin, 1983).

The Notaspidea is a comparatively small order. To the end of 1985, the actual number of described species (including taxa proposed with subordinate status) was 236. No malacologist knows how many biological species exist and regional monographs are sorely needed. The higher classification of the order had turbulent beginnings (summarized by Willan, 1983), but it has now stabilized largely due to Odhner's (1939) and Burn's (1962) thorough taxonomic revisions (see Table 1). The classification of the order

Table 1. Hitherto proposed higher classification of the Notaspidea.

Order Notaspidea Fischer, 1883
    Suborder Umbraculacea Dall, 1889
        Family Tylodinidae Gray, 1847
            Genus *Tylodina* Rafinesque, 1819
            Genus *Tylodinella* Mazzarelli, 1898
        Family Umbraculidae Dall, 1889
            Genus *Umbraculum* Schumacher, 1817
    Suborder Pleurobranchacea Menke, 1828
        Family Pleurobranchidae Menke, 1828
            Subfamily Berthellinae Burn, 1962
                Genus *Berthella* Blainville, 1825
                Genus *Bathyberthella* Willan, 1983
                Genus *Pleurehdera* Ev. Marcus and Er. Marcus, 1970
                Genus *Berthellina* Gardiner, 1936
            Subfamily Pleurobranchinae Férussac, 1822
                Genus *Pleurobranchus* Cuvier, 1805
        Family Pleurobranchaeidae Pilsbry, 1896
            Genus *Pleurobranchella* Thiele, 1925
            Genus *Pleurobranchaea* Meckel in Leue, 1813
            Genus *Euselenops* Pilsbry, 1896

presented in Table 1 is founded on the latest scheme (Burn, 1962) and it incorporates genera described subsequently (Er. Marcus and Ev. Marcus, 1970; Willan, 1983) plus alterations and emendments resulting from papers by Thompson (1970), Baba and Hamatani (1971) and Willan (1977, 1978, 1983). Two suborders, four families and 11 genera are currently recognized (Figs. 1-8).

Much of the literature on notaspidean taxonomy stems from collections made by early exploring expeditions and subsequent literature is widely scattered. The primary literature sources (i.e. those chiefly consulted for distribution of character states) are given in Table 2.

Phylogenetic classifications, as based on Hennigian principles, serve as the best reference systems for the diverse knowledge we now have and are gaining about the evolution of organisms (Hennig, 1966). Their strength lies in their insistence that the taxonomic classification adopted constantly reflect estimates of speciation events in nature (Wiley, 1981). In the past, definitions of higher taxa in the Notaspidea were based on too few (sometimes only one) characters, some of which were homeoplasies, and critical outgroup comparisons were not made so the taxa are unfortunately not amenable to rigorous phylogenetic treatment. As Ev. Marcus and Gosliner (1984) have remarked, incomplete descriptions, which have plagued notaspidean taxonomy, are no longer acceptable. This paper amasses data on 57 qualitative characters and reports the distribution of their states among the eleven notaspidean genera. Primitive and advanced conditions for each character are inferred on the basis of outgroup comparisons. Fortunately this is possible both within the Notaspidea and beyond that to other opisthobranch orders because parallel evolutionary developments have occurred independently many times (Willan and Morton, 1984, p. 9; Gosliner and Ghiselin, 1984). A cladogram is presented, and it is compared with a computer-generated dendrogram of these same data in simple, phenetic form. This paper attempts then, to provide a phylogenetic classification for the Notaspidea (i.e. one that reflects the best estimate of the evolutionary history of the order) (Brundin, 1968).

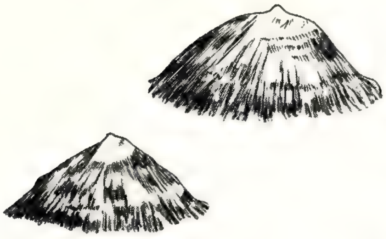
Table 2. Primary literature sources consulted for distribution of character states amongst notaspidean genera.

Genus	Literature Sources
Tylodina	Vayssière, 1883; Mazzarelli, 1898 (as *Tylodinella*); Burn, 1960; MacFarland, 1966; Gosliner, 1981; Ev. Marcus, 1985
Anidolyta nov.	Odhner, 1939 (as *Tylodinella*); Bertsch, 1980 (as *Roya*); Ev. Marcus, 1985
Umbraculum	Moquin-Tandon, 1870; Vayssière, 1885; O'Donoghue, 1929; Pruvot-Fol, 1954; Thompson, 1970; Ev. Marcus, 1985
Berthella	Vayssière, 1898 (as *Bouvieria*); Odhner, 1939; Burn, 1962; Willan, 1984b; Ev. Marcus, 1984
Bathyberthella	Willan, 1983; Willan and Bertsch, 1987
Pleurehdera	Er. Marcus and Ev. Marcus, 1970; Willan, 1984b
Berthellina	Lacaze-Duthiers, 1859 (as "Pleurobranche orangé"); Vayssière, 1898 (as *Berthella*); Bergh, 1905 (as *Berthella*); Gardiner, 1936; Burn, 1962; Ev. Marcus and Er. Marcus, 1967; Thompson, 1970; Willan, 1983
Pleurobranchus	Bergh, 1897, 1898, 1902, 1905; Vayssière, 1898; Thompson and Slinn, 1959; MacFarland, 1966; Thompson, 1970; Ev. Marcus, 1984
Pleurobranchella	Thiele, 1925; O'Donoghue, 1929 (as *Pleurobranchoides*); Eales, 1938; Willan, 1977; Ev. Marcus and Gosliner, 1984
Pleurobranchaea	Bergh, 1897; Vayssière, 1901; MacFarland, 1966; Willan, 1983; Ev. Marcus and Gosliner, 1984
Euselenops	Bergh, 1897, 1905 (as *Oscaniopsis*); Vayssière, 1901 (as *Oscaniopsis*); O'Donoghue, 1929; Ev. Marcus and Gosliner, 1984

METHODS

A set of data for the distribution of 57 qualitative characters was compiled for each of the 11 notaspidean genera listed in Table 1. Characters selected pertain to behavior, body form, mantle, shell, jaws, radula, alimentary and reproductive systems (see Table 3). Characters selected were those that have in the past been considered as taxonomically significant within the order or those which the author believes will be significant in future phylogenetic analyses (e.g. those relating to mantle morphology and behavior that can only be observed or studied in life). Unfortunately characters to do with food or feeding (see review by Willan, 1984a), mantle histology (see review by Thompson and Colman, 1984), sperm ultrastructure (Thompson, 1973; Healy and Willan, 1984), nervous or circulatory systems, or larval studies could not be incorporated because of lack of comparative information. Data on the distribution of character states were collated from personal examinations of the following notaspidean species: *Tylodina corticalis* (Tate); *Umbraculum umbraculum* (Lightfoot); *Berthella pellucida* (Pease); *B. ornata* (Cheeseman); *B. medietas* Burn; *B. americana* (Verrill); *B. martensi* (Pilsbry); *Bathyberthella zelandiae* Willan; *B. antarctica* Willan and Bertsch; *Pleurehdera haraldi* (Er. Marcus and Ev. Marcus); *Berthellina citrina* (Rüppell and Leuckart); *Pleurobranchus grandis* Pease; *P. albiguttatus* (Bergh); *P. forsskali* Rüppell and Leuckart; *P. mamillatus* Quoy and Gaimard; *P. peronii* Cuvier; *Pleurobranchella alba* (Guangyu and Si); *P. nicobarica* Thiele; *Pleurobranchaea maculata* (Quoy and Gaimard); *Euselenops luniceps* (Cuvier). Extensive recourse to the literature was made as well (see Table 2).

Following the method of Hennig (1966), a phylogenetic cladogram was manually constructed for the order. Only unique, derived or "advanced" (apomorphous) characters, as determined in the section on character states, were employed in this analysis and branching systems followed the law of parsimony. This phylogenetic cladogram was then compared with a computer-generated phenetic dendorgram. In amassing the character state distributions to produce this dendogram (Tables 4, 5), no "weighting" of characters as regards their level of relative primitiveness or advancement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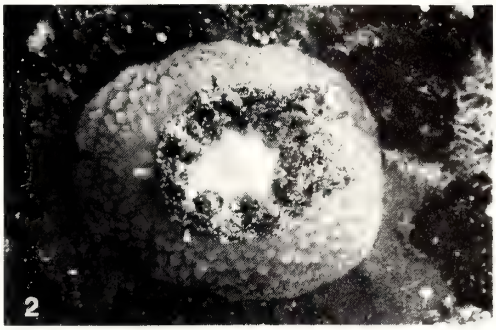
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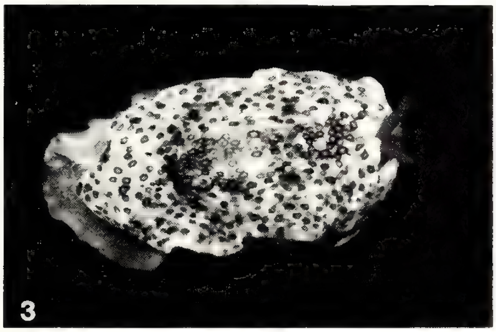
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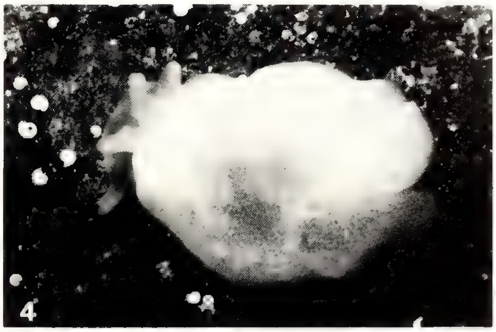
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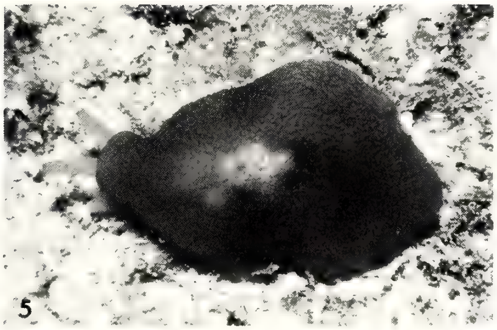
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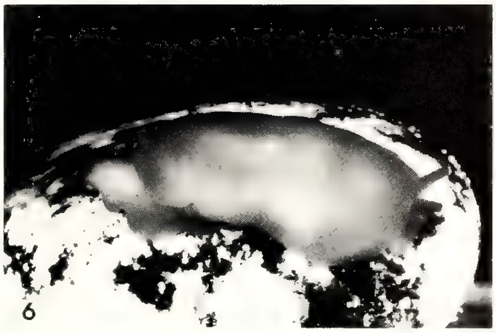
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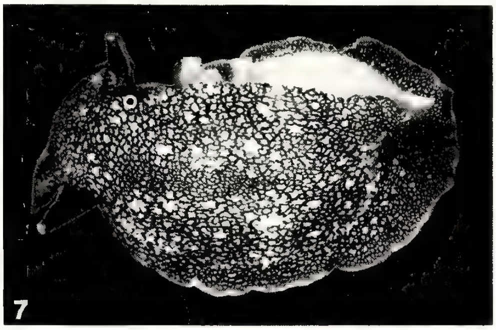
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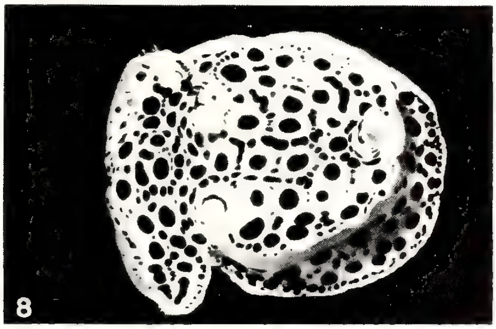
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Figs. 1-8. Type species of notaspidean genera. **Fig. 1.** *Tylodina perversa* (Gmelin): profile of two shells, both 14 mm in maximum length, from Guéthary, near Biarritz, Bay of Biscay, France; redrawn from Pruvot-Fol and Fischer-Piette, 1934: 146. **Fig. 2.** *Umbraculum umbraculum* (Lightfoot): juvenile, extended crawling length of animal 48 mm; found at low tide, Boat Harbour, Cronulla, Sydney, central New South Wales, Australia, 20 May 1979; photograph by R. C. Willan. **Fig. 3.** *Pleurobranchus peronii* Cuvier: length 65 mm; found at low tide, Amity, Moreton Bay, southern Queensland, Australia, 10 November 1981; photograph by R. C. Willan. **Fig. 4.** *Berthella plumula* (Montagu): length 21 mm; found at Knysna, South Africa, May 1984; photograph by T. M. Gosliner. **Fig. 5.** *Pleurehdera haraldi* Er. Marcus and Ev. Marcus: length 40 mm, 3 m, Enewetak Island, Enewetak Atoll, Marshall Islands, 19 September 1981; photograph by S. Johnson. **Fig. 6.** *Berthellina engeli* Gardiner: length 25 mm, found at low tide, Santa Cruz Island, southern California, 23 August 1985; photograph by P. A. Dunn. **Fig. 7.** *Pleurobranchaea meckelii* (Blainville): length 100 mm, 50 m, Gulf of Genoa, Ligurian Sea, northwestern Italy, August 1978; photograph by R. Cattaneo-Vietti. **Fig. 8.** *Euselenops luniceps* (Cuvier): length 60 mm, found at low tide, North Stradbroke Island, southern Queensland, Australia, 29 September 1981; photograph by R. C. Willan.

Table 3. Relative Plesiomorphy and Apomorphy of Characters used for Cladistic Analysis of Notaspidea.

Plesiomorphic	Apomorphic
1. Shell present	Shell absent
2. Shell located externally	Shell internal beneath mantle
3. Shell calcified	Shell without calcification
4. Periostracum smooth, adhering to shell	Periostracum rough, lamellate
5. Muscle scar incomplete	Muscle scar forming a complete ring
6. Shell circular in shape	Shell rectangular
7. Shell (of Umbraculacea) conical	Shell (of Umbraculacea) flattened or plate-like
8. Shell (of Pleurobranchacea) auriculate-oval	Shell (of Pleurobranchacea) spatulate-triangular
9. Shell located centrally relative to body	Shell located anteriorly (rarely posteriorly) relative to body
10. Shell large relative to body	Shell small relative to body
11. Mantle and shell same size	Mantle larger than shell
12. Mantle smooth in texture	Mantle pustulose or puckered
13. Spicules lacking from mantle	Spicules embedded in mantle
14. Anterior border of mantle entire	Anterior border of mantle emarginate or cleft
15. Posterior border of mantle entire	Posterior border of mantle cleft (*Euselenops* only)
16. Mantle margin entire	Mantle margin crenulate (*Tylodinella*) deeply serrate (*Umbraculum*)
17. Mantle incapable of autotomy	Mantle capable of autotomy (Some *Berthella* spp. only)
18. Separation of mantle anteriorly from oral veil	Fusion of mantle anteriorly with oral veil
19. Separation of mantle posteriorly from foot	Fusion of mantle posteriorly with foot
20 One pair of oral tentacles	Two pairs of oral tentacles (*Umbraculum* only)
21. Oral tentacles separate	Oral tentacles joined by oral veil
22. Oral veil relatively narrow with respect to body	Oral veil relatively broad with respect to body
23. Oral veil without papillae	Papillae along anterior edge of oral veil
24.Rhinophores separated (*Umbraculum* only)	Rhinophores together but without any basal fusion (Tylodinidae) Rhinophores together with bases fused (Pleurobranchacea)
25. Rhinophores without rhythmic activity in living specimen	Rhinophoral tips regularly pulsate in living specimen (*Pleurobranchus* only)
26. Upper surface of foot smooth	Upper surface of foot with large pustules (*Umbraculum* only)
27. No pedal gland	Pedal gland present on sole of foot of sexually mature specimens
28. Pedal gland small relative to foot length	Pedal gland large relative to foot length (*Pleurehdera* only)
29. No caudal spur	Caudal spur present posteriorly on upper side of foot (some *Pleurobranchaea* spp. only)
30. Foot without a vertical cleft anteriorly	Foot with a deep, vertical cleft anteriorly (*Umbraculum* only)
31. Gill located in right posterior quadrant of body	Gill extending from left antero-lateral corner of body almost to posterior midline (*Umbraculum* only)
32. Gill attached to body for half its length	Gill attached to body for almost entire length (*Umbraculum* only)
33. Gill with smooth rachis	Gill rachis with row of pustules
34. Anus at posterior end of gill basement membrane	Anus well behind posterior end of gill basement membrane (*Umbraculum* only) Anus in front of end of gill basement membrane
35. Anus opening flush with body	Anus opening at end of anal tube (*Umbraculum* only)
36. Mouth not in pedal cleft	Mouth in vertical pedal cleft (*Umbraculum* only)
37. Buccal mass capable of protrusion during feeding	Buccal mass non-protrusible (*Umbraculum* only)
38. No median buccal (= dorsal accessory) gland	Median buccal gland present
39. Radula with rachidian row	Radula without rachidian row
40. No denticle at base of lateral radular teeth	Single denticle at base (of at least some) lateral radular teeth
41. No accessory denticle on blade of lateral radular teeth	Single accessory denticle on blade of lateral radular teeth (*Pleurobranchaea* only)
42. Lateral radular teeth not lamellate	Two or more denticles on blade of lateral radular teeth (i.e. laterals lamellate)
43. Labial cuticle with two separate thickenings (jaws)	Labial cuticle with a continuous, thickened ring
44. Mandibular elements oval or polygonal	Mandibular elements elongate with a pair of lateral projections (i.e. elements cruciform)
45. Blades of mandibular elements denticulate	Blades of mandibular elements smooth
46. Monaulic reproductive condition (*Tylodina* only)	Diaulic or triaulic reproductive condition

Table 3. (continued)

Plesiomorphic	Apomorphic
47. No flaps surrounding genital apertures	Enlarged flaps surrounding genital apertures in sexually mature specimens (*Pleurobranchus* only)
48. External ciliated, autospermal groove present on penis	No autospermal groove
49. Penis at base of right anterior tentacle Penis on right side in front of anterior end of gill	Penis in vertical cleft in anterior midline, immediately below rhinophores and above mouth (*Umbraculum* only)
50. Penis non-protrusible	Penis able to be protruded for copulation
51. Penis smooth	Penis with papillae on outer surface
52. Two allosperm receptacles present (bursa copulatrix and receptaculum seminis)	One allosperm receptacle only (bursa copulatrix)
53. When two allosperm receptacles are present, the receptaculum seminis arises low down off the vagina near female genital aperture	When two allosperm receptacles are present, the receptaculum seminis arises high up off the vagina near base of bursa copulatrix
54. Prostate gland surrounds or ensheaths autosperm canal or duct	Prostate gland present as a distinct organ
55. No penial gland	Penial gland present
56. Penial sac absent	Muscular penial sac present
57. Vas deferens does not coil within penial sac	Extensive coiling of vas deferens within penial sac

was made. Forty-five of the characters were initially coded as binary attributes (numbers 1, 2, 3, 4, 6, 7, 8, 11, 13, 14, 15, 17, 18, 19, 20, 21, 23, 25, 26, 27, 28, 29, 30, 33, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 47, 48, 50, 51, 52, 53, 55, 56 and 57), nine were coded as disordered multistate attributes (numbers 9, 10, 12, 16, 31, 32, 34, 49 and 54) and four were coded as ordered multistate attributes (numbers 5, 22, 24 and 46). A phenetic analysis using the information statistic "TAXON" program (Ross *et al.*, 1983) was then performed. Thirteen of the characters (numbers 3, 8, 11, 14, 17, 29, 33, 39, 40, 45, 51, 52, 55), originally classified as binary attributes, had to be reclassified as disordered multistate attributes for this computer program because both the two binary states existed together in some genera (e.g. a caudal spur is present in some species of *Pleurobranchaea* but not others) and the program could handle only the 0 or 1 states, not the (0,1) combination.

CHARACTER STATES AND ANALYSES

SHELL

The presence of an external shell in umbraculacean genera was the reason for the early splitting of the Notaspidea into "tectibranch" and "nudibranch" members (Cuvier, 1812, 1817). This artificial partitioning (based on evolutionary grades instead of clades), which denied the existance of an internal shell in pleurobranchs, was soon abandoned as more basic anatomical resemblances came to light. Whilst the shell *per se* of the Notaspidea is unmistakably a plesiomorphy, its actual shape has been much modified from the multispiral form that must have been possessed by the ancestral gastropod that gave rise to this order.

Notaspideans' shells, unlike those of other opisthobranch orders, never display heterostrophy. However, the extreme evolutionary divergence between the two suborders is manifestly evident in their shells. Shells of the Umbraculacea are external and limpet-like (the teleoconch has essentially a circular aperture). The protoconch of both *Tylodina* (Figs. 9-11) and *Umbraculum* (Figs. 12-14) is anisostrophically coiled with the spire (approximately 1.5 whorls) visible to the left of the teleoconch's (and animal's) midline. This sinistrality of the protoconch is evidence of hyperstrophy of larval shells. The only differences between these genera are that in *Tylodina*, the protoconch is narrower with a more elevated axis and the teleoconch is conical whereas in *Umbraculum,* the protoconch is broader and more depressed, its axis is relatively lower and the teleoconch is excessively flattened. The patelliform shell of umbraculaceans (particularly that of *Tylodina* and *Anidolyta*) is remarkably convergent with that of some pulmonates (e.g. siphonariids belonging to the genus *Williamia* (Marshall, 1981; Rehder, 1984). By contrast, shells of the Pleurobranchacea are (in members of the subfamily Pleurobranchinae where they are retained) internal and auriculate (the shell is essentially an exaggerated body whorl) in shape, and coiling is dextral. The larval shell (Figs. 15, 16), which consists of less than one whorl, is slung to the right of the teleoconch's (and animal's) midline. Because both the protoconch and teleoconch coil to the right, the whole shell is orthostrophic. Of course, neither umbraculaceans nor pleurobranchs possess an operculum, so interpretation of the animal's bodily organization must come from studies on larval animal-shell relationships during ontogeny. Then it can be ascertained whether shell shape is due to either anisostrophic coiling or detorsion, or both. Throughout the order, protoconchs are always spirally coiled, that is "type B" of Thorson (1946) and Soliman (1977) or "shell-type 1" of Thompson (1961) (Burn, 1960; Thompson, 1961; Hartley, 1964). The protoconch of umbraculaceans is sinistral revealing, I suggest, an underlying (plesiomorphic) hyperstrophy. That of Pleurobranchaceans is dextral by contrast. This dextrality is certainly an apomorphy and it probably represents a secondary detorsional symmetry imposed on the basic opisthobranch hyperstrophy. This switch in protoconch structure and position, from being relatively multispiral and sinistral

Table 4. Coding scheme for characters used to generate Table 5.

Character No.	Coding
1	0 = absent; 1 = present
2	0 = external; 1 = internal beneath mantle
3	1 = calcified; 2 = without calcification
4	0 = smooth; 1 = rough or lamellate
5	1 = incomplete; 2 = intermediate suspensor present; 3 = complete
6	0 = circular; 1 = rectangular
7	0 = conical; 1 = flattened
8	1 = auriculate; 2 = spatulate
9	1 = anterior; 2 = central; 3 = posterior
10	1 = large; 2 = medium; 3 = small
11	1 = same size; 2 = mantle larger than shell
12	1 = smooth; 2 = pustulose; 3 = puckered
13	0 = absent; 1 = present
14	1 = entire; 2 = weakly emarginate; 3 = deeply cleft
15	0 = entire; 1 = permanently cleft
16	1 = entire; 2 = slightly crenulate; 3 = deeply crenulate
17	1 = absent; 2 = present
18	0 = absent; 1 = present
19	0 = absent; 1 = present
20	0 = one pair; 1 = two pairs
21	0 = separate; 1 = joined
22	1 = very narrow; 2 = narrow; 3 = moderately broad; 4 = very broad
23	0 = absent; 1 = present
24	1 = separated; 2 = together but without basal fusion; 3 = together plus basal fusion
25	0 = absent; 1 = present
26	0 = smooth; 1 = pustulose
27	0 = absent; 1 = present
28	0 = relatively small; 1 = relatively large
29	1 = absent; 2 = present
30	0 = absent; 1 = present
31	1 = well back posterior right; 2 = posterior right; 3 = extending from left corner continuously to posterior midline
32	1 = half length; 2 = less than half length; 3 = almost entire length
33	1 = smooth; 2 = pustulose
34	1 = middle of basement membrane; 2 = in front of hind end of basement membrane; 3 = above hind end; 4 = well behind gill
35	0 = absent; 1 = present
36	0 = mouth not in pedal cleft; 1 = mouth within pedal cleft
37	0 = non-protrusible; 1 = protrusible
38	0 = gland absent; 1 = present
39	1 = absent; 2 = present
40	1 = denticle absent; 2 = present
41	0 = accessory denticle absent; 1 = present
42	0 = lamellae absent; 1 = present
43	0 = cuticularized labial ring; 1 = two separate jaws
44	0 = cruciform; 1 = polygonal
45	1 = smooth; 2 = denticulate
46	1 = monaulic; 2 = diaulic; 3 = triaulic
47	0 = flaps absent; 1 = present
48	0 = absent; 1 = present

Table 4. (continued)

Character No.	Coding
49	1 = anterior midline; 2 = base of right oral tentacle; 3 = on front of gill on right side
50	0 = non-protrusible; 1 = protrusible
51	1 = smooth; 2 = papillose
52	1 = one; 2 = two
53	0 = high; 1 = low
54	1 = absent; 2 = surrounding male duct; 3 = distinct gland
55	1 = gland absent; 2 = present
56	0 = absent; 1 = present
57	0 = vas deferens does not coil within penial sac; 1 = vas deferens coils within penial sac

in Umbraculacea to paucispiral and dextral in Pleurobranchacea is not as great as it might appear. Cox (1960) has demonstrated that all possible states (from hyperstrophic conispiral through planispiral to orthostrophic conispiral) exist in Recent species of the primitive pulmonate family Ampullariidae.

Shells of adult umbraculaceans are covered externally with a tough, adherent periostracum that presumably inhibits encrustacean by marine fouling organisms. When, in *Umbraculum,* the periostracum erodes off the apex, the shell is rapidly colonized by algae, barnacles and serpulid polychaetes that spread over its surface (e.g. Bertozzi, 1983, front cover). Only *Umbraculum* calcifies its shell to any degree. There is a progression in shell musculature, as evidenced by muscle scars on the shell's ventral surface, within the Umbraculacea. *Anidolyta* possesses an incomplete circle of muscle attachments where the dorso-ventral and columellar muscles insert onto the shell; *Tylodina* has a new muscle (intermediate suspensor) in the gap, but the ring of muscles remains incomplete; *Umbraculum* has a complete ring of muscles. I interpret this progression as an ordered series, and have analyzed it as an ordered multistate character.

The mantle cavity has quite disappeared in the Pleurobranchacea. One finds a delicate shell in a shell cavity beneath the mantle in some species of this suborder. The shape of the shell in pleurobranchs is either auriculate (= haliotiform) or spatulate (= triangular). Generally shells of the former shape are relatively large (i.e. they cover the entire visceral cavity) and spatulate shells are small (i.e. they are only one-half to one-fifth the length of the visceral cavity) by contrast. Shell size appears not to be correlated with adult size. The shell is most often located centrally beneath the mantle but there is a tendency for an anterior location in shells of the smaller, spatulate type. All pleurobranch shells are light with meagre calcification and one genus, *Bathyberthella*, is unique because its shell lacks calcification. Sculpture on the shell consists of feeble, concentric growth striae beneath which is a microsculpture of radial punctations or undulating grooves. The shell is never wholly, or even partially, uncovered by the mantle in any pleurobranch when alive (Willan,

Table 5. Character state distribution amongst the genera of the Notaspidea (See Tables 3 and 4 for character names and coding system respectively; * = inapplicable character).

Character No.	*Tylodina*	*Anidolyta*	*Umbraculum*	*Berthella*	*Pleurobranchus*	*Berthellina*	*Pleurehdera*	*Bathyberthella*	*Pleurobranchella*	*Pleurobranchaea*	*Euselenops*
1	1	1	1	1	1	1	1	1	0	0	0
2	0	0	0	1	1	1	1	1	*	*	*
3	2	2	2	2	(1,2)	2	2	1	*	*	*
4	0	1	1	0	0	0	0	0	*	*	*
5	2	1	3	1	1	1	1	1	*	*	*
6	0	0	0	1	1	1	1	1	*	*	*
7	0	0	1	*	*	*	*	*	*	*	*
8	*	*	*	1	1	(1,2)	1	1	*	*	*
9	2	2	2	2	(2,3)	1	1	2	*	*	*
10	1	1	2	(1,2)	(1,3)	3	2	1	*	*	*
11	1	1	1	(1,2)	(1,2)	2	2	1	*	*	*
12	1	1	1	1	3	1	1	1	2	2	1
13	0	0	0	1	1	1	*	0	0	0	0
14	1	1	1	2	3	(1,2)	1	1	*	*	*
15	0	0	0	0	0	0	0	0	0	0	1
16	1	2	3	1	1	1	1	1	1	1	1
17	1	1	1	(1,2)	1	1	1	1	1	1	1
18	0	0	0	0	0	0	0	0	1	1	1
19	0	0	0	0	0	0	0	0	0	1	0
20	0	0	1	0	0	0	0	0	0	0	0
21	1	1	0	1	1	1	1	1	1	1	1
22	1	1	*	2	2	2	2	2	3	3	4
23	0	0	*	0	0	0	0	0	1	1	1
24	1	1	2	3	3	3	3	3	1	1	1
25	0	0	0	0	1	0	0	0	0	0	0
26	0	0	1	0	0	0	0	0	0	0	0
27	0	0	0	1	1	0	1	1	0	1	1
28	*	*	*	0	0	*	1	0	*	0	0
29	1	1	1	1	1	1	1	1	1	(1,2)	1
30	0	0	1	0	0	0	0	0	0	0	0
31	1	1	3	2	2	2	2	2	2	2	2
32	1	1	3	2	2	2	2	2	2	2	2
33	1	1	1	1	2	1	1	1	(1,2)	1	2
34	3	3	4	(1,3)	3	3	3	3	2	2	2
35	0	0	1	0	0	0	0	0	0	0	0
36	0	0	1	0	0	0	0	0	0	0	0
37	1	1	0	1	1	1	1	1	1	1	1
38	0	0	0	1	1	1	1	1	1	1	1
39	2	1	1	1	1	1	1	1	(1,2)	2	1
40	2	1	1	(1,2)	(1,2)	1	2	1	1	1	1
41	0	0	0	0	0	0	0	0	0	1	0
42	0	1	0	0	0	1	1	0	0	0	0
43	0	0	0	1	1	1	1	1	1	1	1
44	*	*	*	0	0	0	0	1	1	1	1
45	*	*	*	(1,2)	2	(1,2)	2	2	2	2	1
46	1	2	*	3	2	3	3	3	2	2	2
47	0	0	*	0	1	0	0	0	0	0	0
48	1	1	1	0	0	0	0	0	0	0	0
49	2	2	1	3	3	3	3	3	3	3	3
50	0	0	*	1	1	1	1	1	1	1	1
51	1	1	1	1	1	1	1	1	(1,2)	1	2
52	1	1	*	(1,2)	(1,2)	2	2	2	1	1	1
53	*	*	*	0	0	1	0	0	*	*	1
54	2	2	3	(1,2)	(1,3)	2	2	2	3	3	1
55	1	1	1	2	1	2	2	(1,2)	1	1	1
56	0	0	0	0	0	0	0	0	1	1	0
57	0	0	0	0	0	0	0	0	1	1	0

1978). It is not uncommon to find individuals of normally-shelled species without a shell. Adults of the genera *Pleurobranchaea, Pleurobranchella* and *Euselenops* lack shells, but Mr. R. Burn has informed me he discovered a tiny shell in a small juvenile *Pleurobranchaea maculata* he was examining. So, absence of a shell in these three genera is interpreted as an evolutionary loss; this synapomorphy for these three genera is homeoplaseous to occasional shell absence in individuals of other pleurobranch genera.

MANTLE

The mantle of umbraculaceans is thin and unremarkable except for *Umbraculum* where its margins are deeply serrate all round. The mantle attains greater morphological diversity in the Pleurobranchidae following its emancipation from the shell; there is a multiplicity of colors (yellow, red, brown, purple) and patterns of boldly contrasting spots. The larger species have tougher mantles and they often possess elaborate, tuberculate ornamentation. These colors, patterns and ornamentations are species-specific. Glands are present within or below the mantle's epithelium (Marbach and Tsurnamal, 1973; histological review by Thompson and Colman, 1984) and small, sub-epithelial spicules occur in the mantles of at least some (probably most) species of *Berthella, Pleurobranchus* and *Berthellina.* The anterior margin of the mantle is usually straight or weakly embayed and it permits extension of the oral veil and rhinophoral tips beyond; it is deeply cleft anteriorly in *Pleurobranchus* and *Berthella* (some species). Some species of *Pleurobranchus* raise the posterior section of the mantle behind the gill (e.g. *P. membranaceus,* Thompson and Slinn, 1959: *P. forsskali*, Thompson, 1970) to allow temporary egress of the respiratory current, but only in *Euselenops* is there a permanent mid-posterior mantle crenulation for this purpose. The mantle of pleurobranchs usually covers the foot entirely (this is certainly the case at rest), or the tail may just appear beneath the mantle in an active animal. (Figs. 17 and 18 illustrate exactly how the mantle/foot relations can alter. The two photographs of the same 48 mm long *Pleurobranchus peronii* were taken in the laboratory less than five minutes apart; the first shows the individual at rest and the second shows it crawling actively.) There are, however, at least two exceptions, *Euselenops luniceps* (where the mantle is a little disc barely half the size of the foot) and *Bathyberthella antarctica* (where the foot extends a considerable distance behind the mantle at all times).

The principal apomorphy exhibited by the subfamily Pleurobranchaeinae is fusion of the mantle with the underlying body. Initial fusion occurs anteriorly between the mantle and head causing the separation of, and consequent lateral displacement for, the rhinophores; this condition is posessed by all species of all the pleurobranchaeine genera. Subsequent fusion takes place posteriorly between the mantle and foot, but this fusion is restricted to a small area; this condition occurs only in some species of *Pleurobranchaea.* Fusion, therefore, takes place in a different sequence in the Notaspidea to that of cladobranch nudibranchs (i.e. members of the superfamilies Dendronotoidea, Arminoidea and Aeolidoidea) where it is first anterior then lateral. Lateral fusion of the mantle and foot (at least on the right side) is obviously impossible in the Notaspidea because of the presence of the gill.

One further consequence of the mantle's emancipation from the shell is increased behavioral versatility. Most pleurobranchs wrap the margins of the mantle around the foot like a cloak when disturbed or lifted off the substratum. Mantle autotomy is known to occur in two species of *Berthella. B. kaniae* can cast off irregular pieces of its mantle when provoked (Sphon, 1972), and, when autotomy occurs in *B. martensi,* it always takes place along "preformed shear zones" (Willan, 1984b).

FOOT

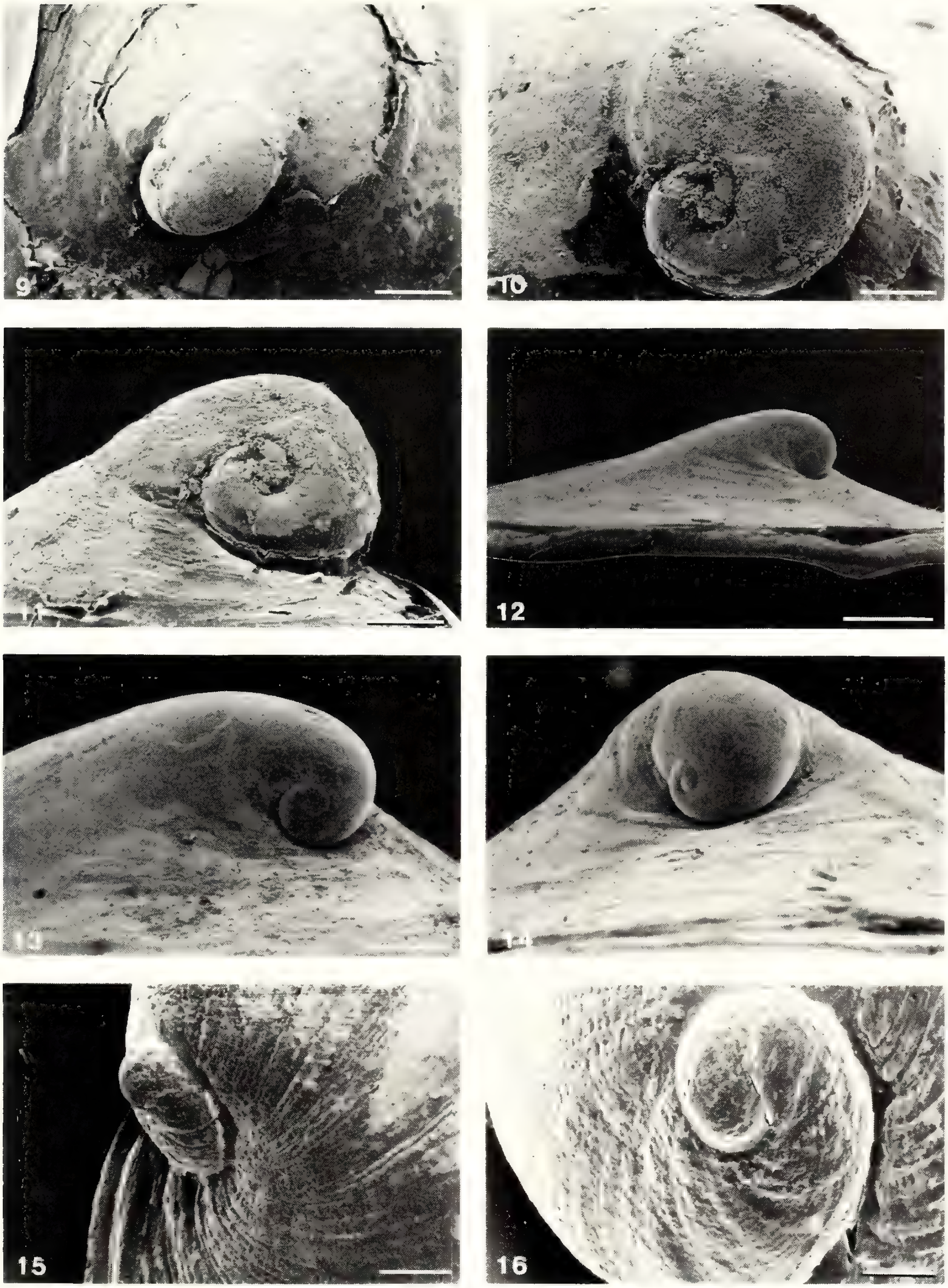
Umbraculum possesses a number of unique features related to its foot. This organ is enormous, tough, entirely covered with pustules and it has a very deep, mid-anterior cleft in which the mouth is located. In the Pleurobranchidae, the foot bears a transverse groove anteriorly (see Fig. 18).

At the rear, a gland is located on the foot sole in all pleurobranch genera except *Berthellina* and *Pleurobranchella.* This pedal gland is shown in Figure 19. It becomes apparent at sexual maturity and probably secretes chemicals for species-specific recognition (Thompson and Slinn, 1959; Macnae, 1962; Willan, 1983). Its occurrence in so many pleurobranch genera would indicate it is a plesiomorphic character, and furthermore, its loss in *Berthellina* and *Pleurobranchella* is not only independent but also secondary. *Pleurobranchus membranaceus,* alone in the order possess the ability to swim by means of its foot; it uses an alternating, flapping movement of the sides of the enlarged foot to propel itself, upside-down, through the water (Thompson and Slinn, 1959).

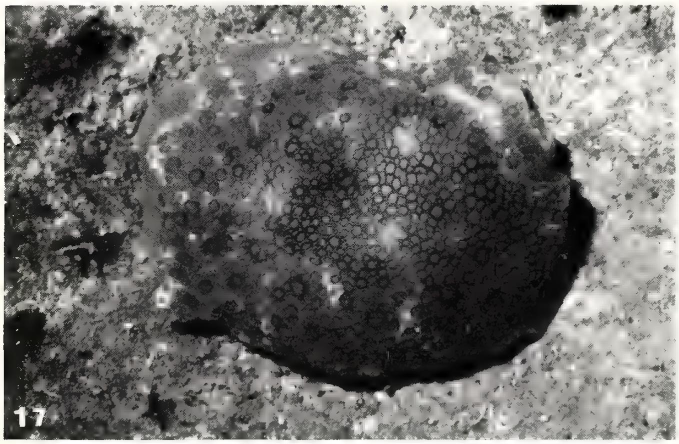
GILL

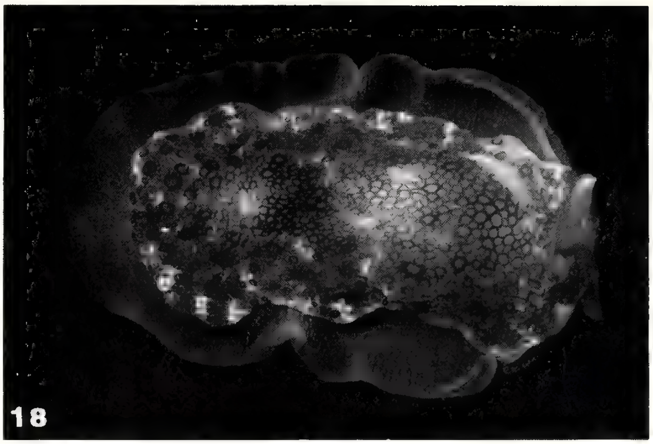
The obvious homologies of the respiratory organ in the Notaspidea, in terms of position, external morphology and direction of blood flow within, present a strong argument for uniting all living side-gilled sea slugs (i.e. notaspideans) within the one order and believing the group to be holophyletic. The terminology of the gill was stabilized by Willan (1983). The central axis of the gill, which lies longitudinally with respect to the body, is the rachis. Side leaves (pinnae), that decrease progressively in size, arise alternately from the rachis and each bears a regular series of fine secondary leaflets (pinnules). The pinnae are symmetric in size between the upper and lower sides of the gill in the Pleurobranchacea and asymmetric in the Umbraculacea.

Thompson and Slinn (1959) and Morton (1972) have shown that ciliary currents direct water between the pinnules. The ciliary currents beat towards the tips of the pinnae. Thompson and Slinn (1959) showed transverse currents across the pinnules whilst Morton (1972) demonstrated downward-directed vertical currents moving fine waste particles between each pinnule and transverse currents at the top and base of each pinna. Within the gill, the efferent branchial vessel runs along the exposed lateral edge and the



Figs. 9-16. Scanning electron micrographs of protoconchs of notaspidean shells. **Fig. 9.** *Tylodina corticalis* (Tate): dorsal view; specimen from 18 m, Julian Rocks, east of Cape Byron, northern New South Wales, Australia; 23° tilt; bar = 200 μm. **Fig. 10.** *T. corticalis:* view from top left showing detail of sinistral coiling; same specimen as in Fig. 9; 47° tilt; bar = 100 μm. **Fig. 11.** *T. corticalis:* left profile; same specimen as in Fig. 9; 84° tilt; bar = 100 μm. **Fig. 12.** *Umbraculum umbraculum* (Lightfoot): left profile showing protoconch and teleoconch of juvenile shell; specimen from Byron Bay, northern New South Wales, Australia (Australian Museum, Sydney, Reg. No. C5279); 90° tilt; bar = 1 mm. **Fig. 13.** *U. umbraculum:* left profile showing detail of sinistral coiling; specimen from Port Jackson, New South Wales, Australia (Museum of Victoria, Reg. No. F11424); 91° tilt; bar = 400 μm. **Fig. 14.** *U. umbraculum:* view from the rear; same specimen as in Fig. 12; 90° tilt; bar = 400 μm. **Fig. 15.** *Berthella pellucida* (Pease): dorsal view showing profile of protoconch; specimen from intertidal reef, Moreton Bay, southern Queensland; 0° tilt; bar = 200 μm. **Fig. 16.** *B. pellucida:* view from posterior right showing detail of dextral coiling; same specimen as in Fig. 15; 45° tilt; bar = 200 μm.





Figs. 17 and 18. Mantle/foot relationships of living *Pleurobranchus peronii* Cuvier. Both photographs depict the same individual (note scar on mantle behind left rhinophore) and were taken less than five minutes apart. Figure 17 shows the animal at rest and figure 18 shows it crawling actively. Specimen (48 mm extended crawling length) from an intertidal pool, Hastings Point, northern New South Wales, Australia, August 1984. Photographs by R. C. Willan.

afferent vessel runs on the mesial edge closest to the body wall (Moquin-Tandon, 1870; Thompson and Slinn, 1959; Morton, 1972). Blood flows within the pinnules in upwards-directed vertical vessels; as many vessels being present as there are pinnules. The rachal tubercles, besides producing mucus, act as "guides" for fine particles, each leading material off the rachis onto the pinna that arises next to it.

The gill is attached to the lateral body wall by two contiguous suspensory membranes. In *Tylodina* and *Anidolyta,* only the anterior half of the gill is attached. Throughout the Pleurobranchidae, the gill is attached for more than half its length. In *Umbraculum,* the gill is attached for almost its entire length. The gill of *Umbraculum* extends from a mid-anterior point on the body in a continuous crescent, around the right side, well back into the right posterior quadrant. Such a situation of extreme branchial enlargement is most unusual and it appears to be another manifestation of the bodily reorganization undergone by *Umbraculum*; one probably necessitated by presence of the flattened, inflexible shell and tough, enlarged foot. The free posterior part of the gill is muscular and mobile in all pleurobranchs (Thompson and Slinn, 1959).

The gill rachis of the Notaspidea is primitively smooth but it bears a series of tubercles in some genera (for example *Pleurobranchus*, see Fig. 19). A tubercle is present on the outer face of the rachis at the point a pinna arises laterally. That tubercles occur on the gill rachis in the otherwise not closely related genera *Pleurobranchus* (where their presence is correlated with the development of tubercles on the mantle) and *Euselenops* (where the mantle is smooth) demonstrates a case of convergent apomorphy. In *Pleurobranchella,* the gill rachis can apparently be smooth or weakly tuberculate depending on the species; however, in the species that do possess them, the tubercles are unlike those of *Euselenops* or *Pleurobranchus*, being merely a series of swellings that are separated by narrow, vertical, somewhat undulating grooves (pers. obs.).

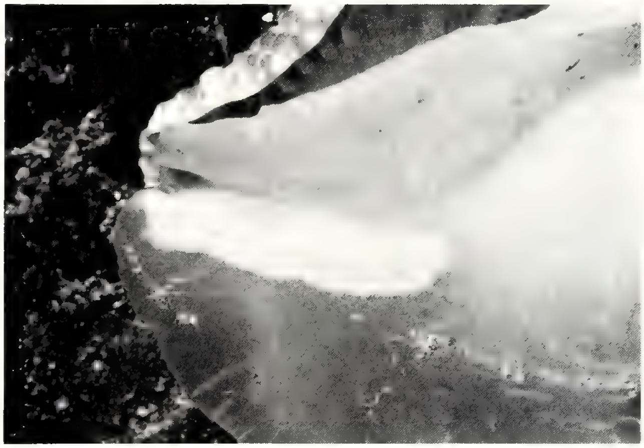


Fig. 19. Pedal gland on posterior foot sole of a living *Pleurobranchus peronii* Cuvier. Note tubercles on gill rachis between mantle and foot. Specimen (86 mm extended crawling length) from an intertidal pool, Hastings Point, northern New South Wales, Australia, February 1984. Photograph by R. C. Willan.

ORAL TENTACLES

In all notaspidean genera bar *Umbraculum,* the oral tentacles and rhinophores possess longitudinal grooves. In all genera but *Umbraculum* again, the oral tentacles are connected to each other by a flap of tissue, the oral veil, that joins them. This veil overhangs the mouth and presumably increases the area sensitive to tactile stimuli and, in fact, all species of *Pleurobranchella, Pleurobranchaea* and *Euselenops* have further enlarged the surface area for touch reception by elaborating compound papillae along the anterior margin of the oral veil. In life, pleurobranchs ripple the oral veil over the surface in an exploratory manner as the animal crawls (Willan, 1983). *Pleurobranchaea* also uses its oral veil to surround and hold prey (Willan, 1984a). The oral veil develops by anterior extension of, and fusion between, the oral tentacles during ontogeny (Usuki, 1969). This oral veil can only be interpreted as one of the symplesiomorphies of the Notaspidea because of its presence throughout the entire order (except *Umbraculum*), even in the most primitive genera *Tylodina* and *Anidolyta*. *Umbraculum* has a remarkable set of oral tentacles that are completely different to any other side-gilled sea slug. It has two pairs of pincer-like oral tentacles at the very base of its muscular foot.

The rhinophores of *Umbraculum* are located side-by-side anteriorly in the midline. This position of the rhinophores represents the symplesiomorphic state too for the Pleurobranchidae and there, it is accompanied by fusion of the basal third of the organs so that they arise from a common base. However in the more advanced Pleurobranchaeinae, the rhinophores are widely separated at the sides of the head because of the ontogenetic fusion of mantle and head to yield confluence of mantle and oral veil. This condition of rhinophoral separation is unquestionably an apomorphy of this pleurobranchaeine group and one would need to follow its ontogeny to determine whether its present condition came about by way of an ancestor like *Tylodina* (where the rhinophores are initially separate during development) or if it was secondary and arose from a pleurobranchine ancestor with closely-positioned rhinophores. Among the Pleurobranchidae, the rhinophores of members of the genus *Pleurobranchus* are noteworthy in that, in living specimens, their tips pulsate regularly; the more active the animal, the faster and more vigorous the pulsations.

GUT

Two regions of the gut present important characters that enable discrimination between taxa. These are the foregut (the pharyngeal bulb in particular) and the hindgut. The parts of major importance are the radula, jaws, median buccal gland and anus.

All members of the Notaspidae have a multiseriate, ptenoglossan radula with numerous rows of (generally) undifferentiated teeth precisely like that suggested for early opisthobranchs (Morton, 1955). A central (or rachidian) tooth is present only in *Tylodina* among the Umbraculacea, and *Pleurobranchaea* and *Pleurobranchella* (some species) among the Pleurobranchacea. Its absence throughout the pleurobranchine genera must therefore, be considered a symplesiomorphy of long standing. The teeth across any particular row are generally similar to each other, although they may differ in size (middle laterals tend to be relatively larger than inner or outer laterals) and shape (inner and middle laterals are broader, whereas outer laterals are narrower and more elongate). Ontogenetic variation within notaspidean radulae parallels that of anthobranch nudibranchs (Bertsch, 1976).

Notaspideans show a widespread tendency to develop secondary denticles on the blade below the cusp of a radular tooth. The position and number of these denticles varies between genera: *Tylodina* bears a single denticle at the base of the main cusp; *Anidolyta* has two or three denticles equally arranged between the cusp and base; *Berthellina* has a row of many (2 to 15) denticles along the distal half of the tooth; *Pleurehdera* has a single denticle located close to the base on inner lateral teeth and it appears in a more and more distal location on progressive outer lateral teeth, at the same time decreasing in height; *Pleurobranchaea* has one (either strong or rudimentary) denticle arising from the base of the cusp. *Umbraculum, Berthella, Pleurobranchus, Bathyberthella, Pleurobranchella* and *Euselenops* never bear secondary denticles (although a small denticle does occur at the base of the tooth in one species of *Pleurobranchs, P. membranaceus*). This diversity of locations and configurations of secondary denticles through the taxa suggests that the Notaspidea primitively had simple, smooth teeth (as in *Umbraculum*) and denticles were acquired later independently in the various lineages, probably concordantly with tooth elongation, to improve feeding efficiency. Certainly the genus with the longest teeth (*Berthellina*) is the one that has the most denticles. I do not think diet canalized tooth structure because, although there are many sponge-rasping notaspideans (i.e. the genera *Umbraculum, Tylodina, Anidolyta, Berthella* and *Berthellina*), there exists a multiplicity of tooth shapes between these genera.

The structure of the labial cuticle presents one of the strongest pieces of evidence in support of a major dictotomy between the two notaspidean suborders. In the Umbraculacea, there is a (variably thickened) cuticularized ring lining the pharyngeal bulb. In the Pleurobranchacea, by contrast, two patches of specialized cuticle (jaws) are present. The jaws are composed of numerous rodlets with flattened, interlocking plates on their inner face. MacFarland (1966, p. 96, 97) has thoroughly described the formation and growth of these mandibular elements, each from a single, large, cuboidal rhabdoblast. These jaws, composed of stacked rodlets, are probably more primitive than the cuticularized ring; Gosliner (1981) envisages the hypothetical opisthobranch ancestor as possessing two well developed jaws. Differences occur between the two subfamilies regarding the shape of the mandibular elements at the jaw's surface; those of the Pleurobranchaeinae are oval or polygonal, whilst those of (most of) the Pleurobranchinae are cruciform with interlocking lateral projections. *Bathyberthella* presents the sole exception to the latter rule; its mandibular elements lack lateral projections and look like those of *Pleurobranchaea* in surface view (Willan, 1983, Figs. 50-53; Willan and Bertsch, 1987, Fig. 6 a-d). I initially suggested that the form of the mandibular elements in *Bathyberthella* might be an example of a retained plesiomorphy linking this genus to the Pleurobranchaeinae, but discovery of a second species in the genus forced a reinterpretation of that view (Willan and Bertsch, 1987). The mandibular elements of *Bathyberthella* must now be viewed as a case of convergence. The anterior margin of oval or polygonal elements (or its homologue, the blade, in cruciform elements) is usally denticulate. This is apparently the case in all genera except *Berthella, Berthellina* and *Pleurehdera* where the blade is smooth. However it is precisely these three genera that show greatest intraspecific and intra-individual variation in this character (Willan, 1984b), so no phylogenetic deductions can be made. Nor, for the reasons of this variability just cited, should taxonomic judgements be based solely on the structure of the mandibular elements. I have already suggested the oval type of mandibular element with denticulate anterior border preceded the cruciform type (Willan, 1983).

The epithelium that lines the anterior section of the stomach ("gizzard") of *Tylodina* has a strong cuticular layer that bears irregular, cuticularized papillae arranged in rows (Vayssière, 1883; Pelseneer, 1894, MacFarland, 1966).

One apomorphic organ possessed by all members of the Pleurobranchidae is a median buccal (= acid or dorsal accessory) gland. The duct of this gland enters the pharyngeal bulb anteriorly on the mid-dorsal surface. The median duct is long and tubular and it branches into a network of fine tubules distally. The tubules are best developed in *Pleurobranchaea* where they can be seen as soon as the body cavity is opened; they ramify extensively between, and are loosely connected to, the viscera (Willan, 1975; Morse, 1984). These tubules are hollow and their tips possess numerous, thin walled, vacuolated cells surrounded by delicate, muscle slips. The cells secrete a highly acidic fluid (pH = 1 to 1.2) which is apparently propelled along the ducts by the muscles and stored in the spongy median duct (Thompson and Slinn, 1959; Thompson and Colman, 1984; Morse, 1984). This duct is extraordinarily long in *Bathyberthella*; in *B. antarctia* it measures about twice the animal's crawling length when fully unravelled (Willan and Bertsch, 1987).

The usual site of debouchement for the anus is just above the posterior end of the gill's suspensory membrane, and this site is presumed to be primitive. However, certain notaspideans have the anal opening in advance of, or behind, this site. The anus opens a short distance in front of the hind end of the basement membrane in all species of the genera *Pleurobranchella, Pleurobranchaea* and *Euselenops.* A minority (about three) of species of *Berthella* have the anal opening directly above the gill within the anterior half of the basement membrane. These genera show no development of an anal tube to direct faeces off the gill. In *Umbraculum* the anus opens on an anal tube, an obvious apomorphy, well behind the rear end of the basement membrane.

REPRODUCTIVE SYSTEM

The Notaspidea possesses a variety of reproductive configurations that encompass all three major evolutionary grades, monaulic, diaulic and triaulic. The monaulic condition seen in *Tylodina* is very primitive. Not only is there a simple, straight-through gonoduct (with only the coelomic section being elaborated into an ampulla), but there is also a non-protrusible cephalic penis bearing an external ciliated groove. *Tylodina* possesses a single allosperm receptacle (i.e. bursa copulatrix) with its opening to the exterior contiguous to that of the undivided pallial gonoduct (MacFarland, 1966). Gosliner (1981) also recognized a second minute allosperm receptacle (i.e. receptaculum seminis) arising off the pallial gonoduct at the point of entry into the nidamental glands. Thus the reproductive system of *Tylodina* "remains essentially unmodified from the hypothetical ancestral (opisthobranch) condition" (Gosliner, 1981).

All remaining notaspidean taxa show (partial or complete) separation of the pallial gonoduct.

All who have studied the reproductive system of *Umbraculum* report a very unusual configuration (Moquin-Tandon, 1870; Ev. Marcus and Er. Marcus, 1967; Ev. Marcus, 1985). The system does need reinvestigating to interpret the homologies of the organs with those of other opisthobranchs and it also needs analysing physiologically to follow the pathways of sperm and eggs as Thompson and Bebbington (1969) have done so thoroughly for *Aplysia. Umbraculum* has its pallial gonoduct divided by an inner, longitudinal fold into seminal and oviducal efferent channels with a prostate gland associated with the former (Ev. Marcus and Er. Marcus, 1967). There are two allosperm receptacles in *Umbraculum. Umbraculum,* like *Tylodina* and *Anidolyta,* has an external penis with ciliated groove (Ev. Marcus and Er. Marcus, 1967). Pruvot-Fol's (1960) belief that the penis (as here designated) of *Umbraculum* was no more than an elaborate genital flap (as in *Pleurobranchus*) from which emerged, terminally, a filiform "true" penis, has not been authenticated. Hartley (1964) has given a brief account of oviposition and early development in *Umbraculum.*

The genera of the Pleurobranchidae fall into two groups depending on the configuration of their reproductive systems. In both groups the reproductive systems are complicated, but this complexity is manifest in different ways. All members of the first group (*Pleurobranchella, Pleurobranchaea, Euselenops*) are diaulic; all have isolated the nidamental glands, reduced the number of allosperm receptacles to one (the bursa copulatrix) and elaborated the terminal male genitalia. In *Pleurobranchella* and *Pleurobranchaea*, the distal vas deferens is greatly elongated and its coils are stowed in a penial sac, an extension of the muscular penial sheath. In both, a distinct, lobed prostate gland is present. All genera of the second group (*Berthella, Berthellina, Bathyberthella, Pleurehdera* and *Pleurobranchus*) have acquired a condition of triauly within their reproductive systems. In all but *Pleurobranchus*, a separate oviduct runs through the nidamental glands. Several other significant features accompany the triaulic condition in genera of this group. Among them are apomorphies like ensheathment of the vas deferens by the prostate gland, absence of an anatomically distinct prostate, acquisition of a penial gland. (This gland, sometimes termed an accessory prostate, is a conspicuous and tubular organ arising from the distal section of the vas deferens close to the penis.) There is also the plesiomorphic persistence of two allosperm receptacles, one of which (the receptaculum seminis) arises high up off the duct of the bursa copulatrix. In the genus *Berthellina*, the receptaculum seminis branches off the vagina high up near the bursa copulatrix; not at the plesiomorphic site close to the vaginal aperture. *Pleurobranchus,* whilst obviously part of this triaulic group, has several apomorphies of its reproductive system. First is the elaboration of the skin surrounding the genital apertures of adult animals into large flaps that presumably function to assist copulation. Second is the reduction, in a few species (previously classified as *Oscanius*), of the number of allosperm receptacles to one (bursa copulatrix). Third is the absence of a penial gland. This gland is also absent in one species of *Bathyberthella (B. antarctica)*, but because all other species and genera close to *Bathyberthella* possess penial glands I interpret its absence in this particular species to be the result of evolutionary loss instead of primary absence. It is presumed that, in *B. antarctica*, a section of the considerably enlarged prostate gland has taken over the function of the penial gland (Willan and Bertsch, 1987).

In contrast to the conservatism of penial structure in members of the Pleurobranchinae, the subfamily Pleurobranchaeinae shows a surprising structural diversity. Some species (of *Pleurobranchaea*) do possess the plesiomorphic smooth penis that lacks any cuticular thickenings. Other species of *Pleurobranchaea* apparently possess either an external cuticle or internal stylet (Ev. Marcus and Gosliner, 1984). Gosliner (1985) claimed that, for the genus *Pleurobranchaea*, penial morphology is species-specific, and no significant change occurs with growth or state of maturity. This contradicts MacFarland's (1966) earlier observations on *P. calilfornica.* A developmental sequence urgently needs to be investigated to substantiate these assertions. Papillae are present on the outside of the penis of *Pleurobranchella* (only sparsely developed) and *Euselenops* (copiously developed).

PHYLOGENETIC HYPOTHESIS

Figure 20 is a cladogram showing inferred phylogenetic relationships amongst the genera of the Notaspidea. Internal nodes (branching points) represent hypothetical ancestors and external nodes (branch tips) indicate extant genera. Numbers besides branches correspond to the characters given in Table 3 and indicate apomorphies (both autapomorphies and synapomorphies) for that particular branch. Where a branch shows an apomorphic trait for a particular character (i.e. it is not possessed by all species), that character is marked with an asterisk. Characters occurring independently in separate lineages (homeoplasies) are not indicated on this cladogram. No attempt has been made to estimate the amount of morphological evolution between taxa, so branch lengths are not proportional to each other.

The Wagner Tree method, on which this analysis is based, hypothesizes a basal separation of the Notaspidea into two phylogenetic lineages that correspond in membership to the established suborders Umbraculacea and Pleurobranchacea. Within the former, *Umbraculum* is separated as a sister group to *Tylodina* and *Anidolyta.* Within the latter suborder [sometimes termed the "higher" Notaspidea (Minichev, 1970)], seven discrete apomorphies argue strongly in favour of the belief of monophyly for the Pleurobranchacea. Here, two major subgroups can be discerned; one consisting of the genera *Pleurobranchus, Berthella, Bathyberthella, Pleurehdera* and *Berthellina*; the other consisting of *Pleurobranchella, Pleurobranchaea* and *Euselenops. Pleurobranchus* forms a sister group to the four remaining genera in the former, and there is a trichotomy (i.e. an unresolved dichotomy) necessitated because *Bathyberthella* shares not a single apomorphy (again it is stressed that this statement relates only to characters employed in this study) with either of its sister groups, *Berthella* or *Pleurehdera/Berthellina. Euselenops* forms a sister group to the two remaining genera

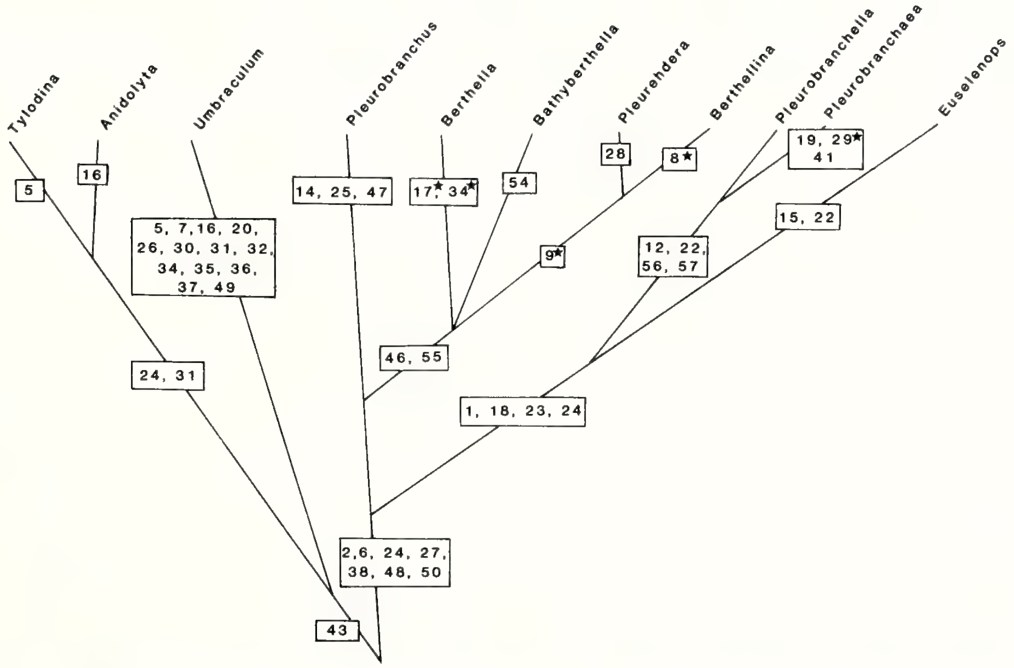


Fig. 20. Cladogram showing phylogenetic hypothesis for relationships between genera of the order Notaspidea. Numbers refer to character transformations listed in Table 3. Asterisks indicate the presence of apomorphic traits (i.e. apomorphies possessed by only some species within that particular genus).

in the latter subgroup.

Strict adherence to the law of parsimony in the construction of this cladogram has necessitated the classification of 12 characters (numbers 4, 10, 11, 12, 21, 33, 34, 40, 42, 51, 53, 54) as homeoplasies. This implies that these characters, which cannot be employed for Hennigian phylogenetic considerations, have been derived independently in different branches of the tree and hence are not unique to any one particular branch. Each of these characters are now explained separately.

Character 4. The plesiomorphic state amongst the Notaspidea is to have a thin periostracum that adheres closely to the shell. But in two of the Umbraculacean genera (*Anidolyta* and *Umbraculum*) the periostracum is scale- or beard-like. *Tylodina*, the genus most closely related to these two retains a smooth, adherent periostracum.

Characters 10 and 11. The shell has been reduced in size, independently it would appear, in each of the major notaspidean lineages. So presence of a medium- to small-sized shell, as in *Tylodina, Umbraculum, Berthella* (some species), *Pleurobranchus* (most species), *Berthellina* and *Pleurehdera* does not indicate phylogenetic affinity. It should be noted that both the body to shell ratio (character 10) and body to mantle ratio (character 11) show apomorphic traits in two genera (*Berthella* and *Pleurobranchus*).

Character 12. The plesiomorphic state of the mantle throughout the Notaspidea is to be smooth-textured. Yet in three genera (*Pleurobranchus, Pleurobranchella* and *Pleurobranchaea*) the mantle is pustulose. That this ornamentation has been derived independently is evident when its structure is examined in detail. The mantle of *Pleurobranchus* has regular, rounded tubercles (mamillae) that are conical or flat-topped; that of the other two genera is irregularly puckered by minute, intersecting ridges or folds.

Character 21. The development of a veil anteriorly between the oral tentacles is a derived condition adopted, it would appear, very early on in the evolution of the Notaspidea. Its absence alone in *Umbraculum* might well be secondary (in which case it would be a plesiomorphy for the whole order). At this time I view the moderately extended tissue connection between the base of the oral tentacles (the "buccal shield" of MacFarland, 1966) of *Tylodina* and *Anidolyta* as homologous with the enlarged, sail-like construction that unites the oral tentacles of all pleurobranchs.

Character 33. The texture of the outer surface of the gill's rachis in the Pleurobranchinae is correlated with that of the mantle's surface (they are probably under the same genetic controlling mechanism), i.e. *Pleurobranchus* always has a tuberculate rachis and mantle and both are always smooth in all the other genera. However in pleurobranchaeine genera that have irregularly textured mantles (*Pleurobranchella* and *Pleurobranchaea*), the same relationship does not hold. In *Pleurobranchella* the gill rachis is variable (tubercles are present in *P. alba* but not in *P. nicobarica* (pers. obs.), and in the smooth-mantled *Euselenops*, the rachis is tuberculate.

Character 34. With the exception of *Umbraculum* (where the posterior anal position is obviously derived), the Notaspidea mostly have the anus opening at, or close to, the rear of the gill's suspensory membrane. There appears to have been a trend, in the Pleurobranchacea, for the progressive forward movement of the anus. *Berthella* shows apomorphic traits (see the section on character analyses above) and all genera of the subfamily Pleurobranchaeinae have the anus in front of the hind end of the gill. The different anal positions in these two lineages indicate the homeoplaseous nature of this character.

Character 40. As explained earlier, species from the following genera possess a small denticle at the base of the inner face of, at least some, lateral teeth in their radula: *Tylodina; Berthella; Pleurobranchus; Pleurehdera.* These denticles vary in their precise position and magnitude as could be expected from a homeoplaseous character. It is noteworthy that this character is variable between two pairs of closely-related sister genera (i.e. present in *Tylodina* but not *Anidolyta;* present in *Pleurehdera* but not *Berthellina*).

Character 42. The plesiomorphic condition amongst the Notaspidea is to have simple radular teeth without additional denticles. However, throughout the order, lineages have independently acquired such structures. The presence of denticles reaches its zenith in *Berthellina* where teeth are greatly elongate and can possess up to 15 denticles on the distal half of their blades. Since similar denticles are present, though fewer in number in *Pleurehdera*, one can assume the character is an autapomorphy for that sister group. Yet, similar denticles are present on the teeth of *Anidolyta* and there they must be regarded as homeoplaseous.

Character 51. Penial papillae appear to have evolved independently in two genera of the Pleurobranchaeinae, *Pleurobranchella* (shows apomorphic traits) and *Euselenops.* The detailed structure of the penial papillae and their arrangement is not precisely the same in these genera, their presence probably being related to species-specific morphology of the reproductive tract.

Character 53. The plesiomorphic position for the receptaculum seminis is low on the vagina near the female genital aperture when two allosperm receptacles are present. The point of origin is located further up the vagina in *Berthellina* and *Euselenops*, an independent shift it would seem.

Character 54. The distribution amongst notaspidean genera of character states relating to the prostate gland is confused. Prostatic tissue either ensheaths the male efferent duct or forms a distinct, lobed gland; mutually exclusive conditions it would appear. But the distinction is not so clear cut when individual genera are considered (see Table 4). A prostate gland is apparently absent in *Berthella* (some species), *Pleurobranchus* (some species) and *Euselenops.* It ensheaths the vas deferens in *Tylodina* and *Anidolyta* (in both it is not anatomically distinct), *Berthellina, Berthella* (some species), *Pleurehdera* and *Bathyberthella.* It occurs as a distinct gland in *Umbraculum, Pleurobranchus* (some species), *Pleurobranchella* and *Pleurobranchaea.* The trend throughout all the lineages then, is towards separation off of the prostatic tissue from the vas deferens to form a distinct gland. This process appears to have occurred independently in all clades but the *Berthella/Bathyberthella/Pleurehdera/Berthellina* one. Some of the confusion about this character may have arisen through inadequate early descriptions of reproductive systems and histological studies are now required to delineate the extent and relationships of the prostatic section of the male duct.

Apomorphies need not only be specialized characters that a taxon possesses. Apomorphies can be manifested also by losses, and amongst the Notaspidea there are four cases (character numbers 27, 39, 45, 52) where lineages or branch tips have independently lost structures. All four are extremely important in phylogenetic considerations and they are now discussed separately.

Character 27. Possession of a pedal gland by sexually mature animals is a symplesiomorphy of the Pleurobranchidae and so its absence in two otherwise distinct genera, *Berthellina* and *Pleurobranchella*, argues for independent loss.

Character 39. Most lineages of notaspideans have no central (rachidian) tooth in their radulae. I believe this absence is due to independent loss.

Character 45. Earlier in this paper I postulated that the ancestral condition amongst the pleurobranchs was to have denticulate anterior borders (= blades) to the jaw's mandibular elements. In this case, outgroup comparison is impossible because the Umbraculacea lack mandibular elements completely. Therefore I consider the smooth-bladed condition of the mandibular elements as is found in *Berthella* (some species), *Berthellina* (most species) and *Euselenops* to have occurred independently by simplification from the ancestral (denticulate) condition.

Character 52. The plesiomorphic condition in the Notaspidea is to possess two allosperm receptacles (bursa copulatrix and receptaculum seminis), however several lineages have independently reduced that number to one by loss of the receptaculum seminis. Loss of the receptaculum has occurred throughout all of the Pleurobranchaeinae whilst in *Tylodina*, *Berthella* and *Pleurobranchus* apomorphic traits for its loss are evident.

One anomalous character (number 44) deserves further note. Apart from *Bathyberthella*, the disposition of character states relating to mandibular elements is straightforward throughout the major lineages, i.e. cruciform in pleurobranchine lineages and polygonal in pleurobranchaeine lineages. *Bathyberthella* is clearly an exception and the significance of its elongate-polygonal mandibular elements, already touched on in a previous section, is discussed further in the forthcoming section on generic evaluation.

PHENETIC ANALYSIS

The dendrogram resulting from the "TAXON" program is presented in Figure 21. It agrees extremely well with the manually derived phylogenetic cladogram that I have presented earlier in this paper (Fig. 20). The dendrogram clearly distinguishes three clusters of genera in the order corresponding to the taxa Umbraculacea, Pleurobranchinae and Pleurobranchaeinae. Note that this strictly dichotomous program links *Berthella* with *Bathyberthella*. According to this analysis, the two genera with greatest affinity (i.e. most characters in common) are *Pleurobranchella* and *Pleurobranchaea*.

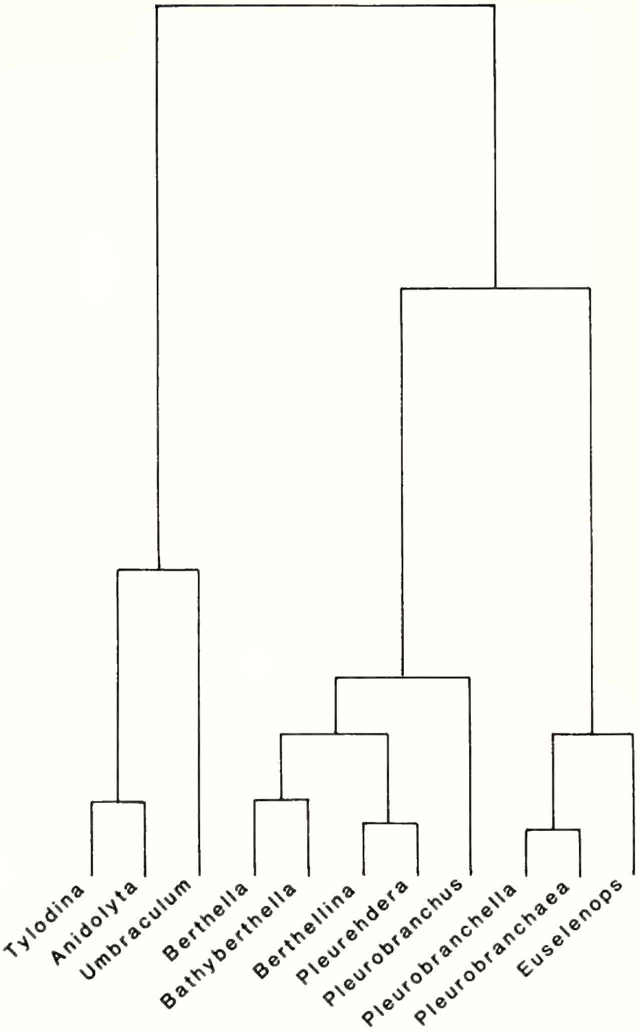


Fig. 21. Phenetic analysis of relationships between genera of the order Notaspidea. Dendrogram results from application of 'TAXON' computer program to data in Table 5.

This "TAXON" program was able to identify the most useful discriminating attributes between groups in the hierachy. Those singled out for distinguishing between the Umbraculacea (3 members) and Pleurobranchacea (8 members) were shell position, shell shape, oral veil width, gill location, median buccal gland, labial cuticularization, autospermal groove, and penial position. Chief discriminators between the Pleurobranchinae (5 members) and Pleurobranchaeinae (3 members) were shell presence /absence, anterior fusion of mantle and head, oral veil width, papillae on oral veil, relationships of the rhinophores, anal position, mandibular element shape and penial gland. Chief discriminations between the Tylodinidae (2 members) and Umbraculidae (1 member) were shell length to height ratio, shell length to body lenth ratio, mantle texture, mantle margin, number of pairs of oral tentacles, connection of oral tentacles by an oral veil, texture of dorsal surface of foot, vertical anterior cleft in foot, anal tube, position of mouth and protrusibility of buccal mass. Attributes discriminating between *Pleurobranchus* and the remaining pleurobranchine genera (4 members) were mantle texture, activity of rhinophoral tips, genital flaps, shape of prostate gland and penial gland. Attributes discriminating *Euselenops* from the remaining two pleurobranchaeine genera were mantle texture, posterior mantle border, anterior margin of mandibular elements, muscular penial sac, and coiling of the vas deferens. Attributes cleaving the Pleurobranchidae (apart from *Pleurobranchus*) into two groups each containing two genera were shell location, shell length to body length ratio, size of pedal gland, and numbers of denticulate lateral teeth in the radula. Attributes discriminating between the genera *Tylodina* and *Anidolyta* were nature of periostracum, mantle margin, rachidian teeth and numbers of denticulate lateral teeth in the radula. Attributes discriminating between the genera *Berthella* and *Bathyberthella* were shell calcification, mantle spicules, anterior border of mantle and shape of mandibular elements. Attributes discriminating between the genera *Berthellina* and *Pleurehdera* were shell length to body length ratio, pedal gland and relative position of receptaculum seminis. Finally, the attributes discriminating between the genera *Pleurobranchella* and *Pleurobranchaedae* were posterior mantle/foot fusion, pedal gland and presence of accessory denticles on radular teeth.

The "CRAMER" routine of the "TAXON" program was run to explore possibilities of groupings other than those presented in the dendogram. That "CRAMER" was largely unsuccessful adds more credibility to the original dendorgram. "CRAMER" did suggest an alternative grouping for *Pleurobranchus*; that genus became allied to the subfamily Pleurobranchaeinae on the grounds of reproductive condition and lack of a penial gland.

DISCUSSION

REAPPRAISAL OF FAMILIES

The great similarity between the phylogenetic cladogram (Fig. 20) and phenetic dendrogram (Fig. 21) suggests that, given the character set used here, the hypothesis these analyses supports has a high probability of being the correct one. That this hypothesis has been corroborated is gratifying when one recalls that for any 11 taxa, the possible number of rooted phylogenetic trees with labelled tips and with unlabelled interior nodes is 6.9×10^9 (Felsenstein, 1978). Additional support for the basic lineages of this hypothesis has come from recent investigations on notaspidean sperm ultrastructure (Healy and Willan, 1984) and diet (Willan, 1984a).

The evidence (from shell, gut, mantle-gill complex and reproductive system) overwhelmingly points to a monophyletic origin for the Notaspidea. Two Russian workers, Minichev and Starobogatov (1978), proposed a polyphyletic derivation for the group and erected the new orders Umbraculida and Pleurobranchida belonging to the (newly constituted) subclasses Dexterobranchia and Opisthobranchia respectively. Their hypothesis rested entirely on characters of the mantle-gill complex and protoconch. In the following year, these same authors proposed a sweeping reclassification of higher taxa in the Opisthobranchia *sensu* Minichev and Starobogatov in a short paper written in Russian (Minichev and Starobogatov, 1979). This reclassification has only recently been published in English (Minichev and Starobogatov, 1984). It purports to use the reproductive system to support grandiose elevation of taxa; the pleurobranchs are raised to an order (Pleurobranchida) containing three suborders (Pleurobranchina, Berthellinina and Berthelleina), the latter two newly named. Nowhwere do the authors state the particular genera contained within their suborders and even worse, nowhere do they present or give reference to, the anatomical data on which their systems are based. To indicate the futility of new classifications and taxonomic inflation based on single systems, I will disprove the characters to which Minichev and Starobogatov attributed so much importance by showing them to be false. Minichev and Starobogatov's account of protoconchs is incorrect; those of the Umbraculacea are actually hyperstrophic. Many species of *Berthella* do not possess a connection (a special vaginal duct) between the vagina and oviduct; the condition varies within genera. Finally, similar mantle-gill relationships are also found in the Runcinacea and Thecosomata, so that character is homeoplaseous. What is needed now is comparative anatomical data not more higher taxa.

Despite the confusion brought about by unsupported taxonomic inflation, the available data do emphasize the separation of the Notaspidea into two subgroups. This basic separation is evidenced by the great differences in buccal cuticularization, shell morphology, gill location, male efferent canal, penial position, median buccal gland and penial gland. Each group has been traditionally considered as a suborder (i.e. Umbraculacea and Pleurobranchacea), and I think that is still the best taxonomic level to treat them at.

Within the Umbraculacea there is again a major dichotomy; *Tylodina* and *Anidolyta* being fused together to one side and *Umbraculum* to the other. As I will expand on the genus *Umbraculum* in the subsequent section, there is no need to outline here the very many specialized, derived characters possessed by that genus and (monotypic) family. Suffice to say that the Umbraculidae well merits separation, at the family level, from its sister tylodinid group. This is the more generally accepted position in the literature (e.g. Pruvot-Fol and Fischer-Piette, 1934; Pruvot-Fol, 1954; Burn, 1962; Thompson, 1970; Odhner in Grassé, 1968; Rehder, 1980; Bertsch, 1980; Ev. Marcus, 1985; Cattaneo-Vietti, 1986). I now readily recant from the position taken in an earlier publication (Willan, 1983) wherein I grouped the Umbraculidae and Tylodinidae together as a single family. My basis for doing so was Thiele's (1931) scheme of classification for the Opisthobranchia. Thiele followed Pilsbry (1896). Other authors who did not distinguish separate families in the suborder Umbraculacea have been Ghiselin (1965), Keen (1971), Thompson (1976) and Gosliner (1981).

Delineation of taxa at the family-level group within the

Pleurobranchacea (i.e. the "higher" Notaspidea of Minichev, 1970) is less straightforward. Following Odhner (1926), all genera of the Pleurobranchacea were placed in a single family, Pleurobranchidae, and this remains the most widely accepted classification (e.g. Pruvot-Fol, 1954; Er. Marcus, 1965; Thompson, 1970; Ev. Marcus and Er. Marcus, 1970; Willan, 1983, 1984b; Healy and Willan, 1984; Willan and Bertsch, 1987). But, following Burn (1962), a few authors treat the genera as comprising two (somewhat unfortunately named), separate families, Pleurobranchidae and Pleurobranchaeidae (Ev. Marcus, 1977; Ev. Marcus and Gosliner, 1984; Gosliner, 1985; Cattaneo-Vietti, 1986). Not one of these subsequent authors have discussed their basis for recognizing separate families or advanced further arguments to support it. Burn (1969) reverted seven years later to using one family, Pleurobranchidae, to encompass all pleurobranch genera and he continues to hold this view to the present time (R. Burn, pers. comm., 1986). I hope this paper sets forth sufficient reasons in support of the single family stance to convince other malacologists of its correctness.

The monophyletic origin of the Pleurobranchacea has never been challenged, based soundly as it is on many characters, apomorphies being: the internal, rectangular shell; presence of pedal gland; median buccal gland; internal, tubular vas deferens; protrusible penis. What is debated is the taxonomic category best suited to the two major pleurobranch subgroups. The characters splitting the Pleurobranchidae are: presence or absence of a shell; anal position; transverse width of oral veil, relationships of the mantle and head; location of rhinophores; papillae lining oral veil; mandibular element shape; presence or (secondary) absence of pedal gland. Only the third, fourth, fifth and sixth of these characters are apomorphies of the pleurobranchaeine branch (consisting of three genera) and none is an autapomorphy for the pleurobranchine branch (five genera). Outgroup comparison for the pleurobranchaeine branch reveals every one of the four apomorphies occurs (in whole or as apomorphic traits) in genera of the pleurobranchine branch [i.e. (i) shell-less *Berthellina* and *Pleurobranchus* species, (ii) forward anal position in *Berthella*, (iii) elongate-polygonal mandibular elements in *Bathyberthella*, and (iv) absence of a pedal gland in *Berthellina* and *Bathyberthella*]. Therefore, the essential divisions between the two pleurobranch subgroups are reduced to four, of which the three most important are interdependent (i.e. one cannot occur without the simultaneous occurrence of the other two). In this clade, fusion of the mantle and head anteriorly necessitated separation of the rhinophores and, as a consequence, the oral veil spread transversely. This being the case I find no grounds for recognition of separate families. I have already shown the division could not be justified on the characters Burn (1962) originally chose (Willan, 1983). Two of the characters employed by Burn in his definition of the separate families were: (i) gill rachis - smooth or transversely grooved (Pleurobranchidae), or tuberculate (Pleurobranchaeidae); (ii) mantle - generally larger than the foot (Pleurobranchidae), or generally smaller than the foot (Pleurobranchaeidae). Both are simply incorrect. To counteract the first point is the fact that all members of the genus *Pleurobranchus* have a strongly tuberculate gill rachis. To counteract the second point are the facts that, in life, species of *Pleurobranchella* have a mantle that is larger than the foot (Ev. Marcus and Gosliner, 1984), and this is also true for *Pleurobranchaea obesa* (Gosliner, 1985); also *Bathyberthella antarctica* has a foot that is much larger than its mantle (Willan and Bertsch, 1987). Neither character, therefore, can be used to separate clusters of genera at any higher level whatsoever. Erzinclioglu and Unwin (1986) oppose, on philosophical grounds, the elevation of subfamilies to families.

In a later paper, Odhner (1939) recognized two subgroups within the Pleurobranchidae (as recognized by him). One (the berthelline group) being (to use the original definitive characters) small-sized with simple, non-tuberculate gill rachis, and the other (the pleurobranchine group) being large-sized with a tuberculate gill rachis. According to current concepts of generic boundaries, the genera *Berthella, Berthellina, Bathyberthella* and *Pleurehdera* would constitute the former group and *Pleurobranchus* would constitute the latter one by itself. Such a division based on relative size in conjunction with mantle and gill rachis texture cut right across the earlier scheme of Vayssière (1897, 1898) which united *Berthella* and *Pleurobranchus* and excluded *Berthellina.* This was because it was essentially based on radular characteristics. One of the principal objectives of my phylogenetic studies has been to evaluate these conflicting classifications.

To date, my investigations (on phylogenetics, phenetics, sperm ultrastructure and diets) all vindicate Odhner's (1939) scheme and they confirm the berthelline and pleurobranchine groups are natural, holophyletic clusters of genera. To complement the characters (of relative size, and mantle and gill rachis surface texture) originally used by Odhner, I have identified several additional significant ones. The group of berthelline genera has synapomorphies of triaulic reproductive condition and penial gland. The other lineage (*Pleurobranchus*) has autapomorphies of deep anterior mantle cleft, rhinophoral pulsating activity in life, permanently exposed flaps surrounding the genital apertures of sexually mature animals, and tuberculate mantle and gill rachis. The acrosome of *Pleurobranchus* sperm is clearly periodically banded, the nucleus is relatively short, up to five nuclear keels are present and the glycogen piece is relatively short. In all the berthelline genera, the acrosome is not periodically banded (or very weakly so), the sperm nucleus is relatively long, there is a single nuclear keel or none at all and the glycogen piece is relatively long (Healy and Willan, 1984). All *Pleurobranchus* species presently known specialize on ascidians whereas the berthelline genera eat sponges [although one species, *Berthellina citrina*, is also able to eat scleractinian corals and sea anemones (Willan, 1984a)]. Burn (1962) formalized Odhner's system by naming these two lineages as new subfamilies, Berthellinae Burn and Pleurobranchinae Férussac. The characters discussed above, whilst confirming the existence of separate lineages, should not, I suggest, be used to justify subdivision at the subfamily level. That rank is too high and I recommend a ranking of tribe is more appropriate; thus the two tribes should be called Berthellini Burn and Pleurobranchini Férussac.

One final point strengthening my argument for not elevating the taxonomic status of the bertheIline and pleurobranchine groups to the level of subfamilies concerns relative body size. Burn (1962) used this character in his classification. Because it is a more subjective character than others, it should be considered apart from them. Relative size is probably valid to use to separate adults of most species of the Pleurobranchinae (i.e. *Pleurobranchus* species tend to attain 70 to 300 mm and are therefore "large" compared to members of the other genera that are "small" with sizes of 20 to 70 mm). It must, however, be remembered that we are dealing with highly deformable invertebrates that have indeterminate growth. For this reason, size cannot be used as a strict (and certainly not exclusive) taxonomic character. Several exceptions are already known that lessen its usefulness. For example, there are "small" species of *Pleurobranchus* (less than 70 mm crawling length - *P. ovalis*) and a species of *Bathyberthella* grows to over 120 mm in Antarctic waters (Willan and Bertsch, 1987).

Before leaving this section on families, I must highlight one alteration it has been necessary to incorporate into the taxonomic hierachy given in Table 1. Authorship of the family Pleurobranchidae is usually credited to Menke, 1828, but it was actually introduced by Férussac (as "Les Pleurobranches") six years earlier (Férussac, 1822, pp. 26 and 29). Therefore, according to the principle of co-ordination embodied in the International Code of Zoological Nomenclature (I.C.Z.N., 1985, Article 36), authorship of the subfamily Pleurobranchinae and tribe Pleurobranchini must also be attributed to "Férussac, 1822".

REAPPRAISAL OF GENERA

This is the section where I break ranks with strict cladists and employ judicious weighting of characters to obtain the "most correct" relationships between genera. All the eleven genera given in Table 1 are considered separately in this appraisal. The characters defining each are briefly enumerated and examined so as to consider relationships to other genera. Where necessary, the consideration ranges to reappraisals of synonymous taxa. In light of what has already been written in this paper, I feel that complete diagnoses, or even listing sets of apomorphies, for every genus would be profligate. The only exception is *Anidolyta* where a formal diagnosis has to be provided because a new taxon is being proposed. The sequence of presentation is phylogenetically systematic, starting with the most primitive genus and progressing to the most advanced.

Tylodina Rafinesque, 1819

Type species, by subsequent designation (Pilsbry, 1896, p. 185), *Tylodina citrina* Joannis, 1834 (= *Patella perversa* Gmelin, 1790). Recent, Mediterranean Sea. Fig. 1.

Synonyms: *Parmophorus* Cantraine, 1835; *Joannisia* Monterosato, 1884; *Tylodinella* Mazzarelli, 1898.

This genus is unquestionably the most primitive in the order Notaspidea and among the most primitive of the entire Opisthobranchia. This view is primarily based on the structure of the nervous and reproductive systems. The central nervous system consists of a ring of five discrete ganglia, two cerebral, two pleural and the visceral ganglion, the latter retaining its integrity (Vayssière, 1883; MacFarland, 1966; Gosliner, 1981). The reproductive system is monaulic with an external sperm groove leading from the genital aperture at the base of the right oral tentacle to the non-protrusible penis. Another very primitive feature is the osphradium. This organ (merely a small patch of sensory epithelium, lying close in front of, and slightly below, the anterior end of the gill rachis) was first described histologically by MacFarland (1966). The osphradium is ennervated by a separate ganglion located immediately beneath it (Pelseneer, 1894; MacFarland, 1966). *Tylodina* possesses many other plesiomorphies for the order, the more significant of which are: the external shell; velar connection (albeit small) between the laterally slit oral tentacles; separate, dorso-ventrally slit rhinophores; smooth upper foot surface; presence of a pedal gland; gill location; smooth gill rachis; absence of a median buccal gland; two allosperm receptacles. *Tylodina* does possess some apomorphies however, these are to do with shell musculature, cuticularized labial ring, cuticularized papillae in anterior section of stomach and penial position. The last three of the characters just mentioned are, in fact, synapomorphies for *Tylodina* and its sister genus *Anidolyta*. The single apomorphy I can find for *Tylodina* is the interpolation of a special intermediate suspensor muscle in the gap between the ends of the crescentic columellar muscle.

Biogeographically, *Tylodina* is an enigmatic genus. Five species occupy restricted ranges in temperate waters, *T. perversa* in the eastern Atlantic and Mediterranean, *T. americana* in the western Atlantic, *T. fungina* in the eastern Pacific, *T. corticalis* in southern Australia, *T. alfredensis* in southern Africa. Only minor differences separate these species and, in fact, the characters separating them at the specific level are uncertain. Whilst I think Thompson (1970) was incorrect in suggesting all these species be merged into one, I do accept the opinion of Pruvot-Fol and Fischer-Piette (1934) that all the nominal taxa based on Mediterranean specimens are synonymous.

Anidolyta gen. nov.

Type species, here designated, *Tylodina duebeni* Lovén, 1846. Recent, North Atlantic Ocean.

Synonyms: *Tylodina* Lovén, 1846 (non Rafinesque, 1819); *Roya* Bertsch, 1980 (non Iredale, 1912).

Diagnosis: Small notaspideans bearing an external, oval, patelliform shell (approximately 10 mm in length). Mantle margin crenulate or minutely papillate. Columellar muscle crescentic; incomplete on right side; gap not filled by intermediate suspensor. Oral tentacles slit laterally; joined to each other by a small veil (buccal shield). Rhinophores slit dorso-ventrally; without any proximal connection. Gill a short plume on right side; attached to body for half its length. Genital apertures at base of right oral tentacle. Radula broad, ptenoglossan; rows lacking a rachidian; laterals very numerous, bearing 2 or 3 strong denticles on blade below cusp, not showing differentiation across rows.

Anidolyta remains the most enigmatic genus of the order. In the first place this is due to the scarcity of specimens, less than five being known. Actually all published descriptions rely on only three, i.e. the holotype of *Tylodina duebeni* (Odhner, 1939) and two *Roya spongotheras* (Bertsch, 1980). In addition to this difficulty, is the problem of the genus' confused taxonomic history. Odhner (1939) placed Lovén's *Tylodina duebini* in the genus *Tylodinella* Mazzarelli on account of Mazzarelli's (1898) published description. I am certain Mazzarelli's account of his *Tylodinella trinchesii* relates to a juvenile *Tylodina perversa.* The similarities are overwhelming: pale yellow animal; thin, circular, conical shell; small oral veil; eyes; position of gill, anus and penis; structure of gill, radula and central nervous system; division of stomach into anterior cuticularized and posterior thin-walled regions. The fact that the animal of *Tylodinella trinchesii* could be completely accommodated within its shell merely indicates it was a juvenile specimen and its immaturity must have resulted in Mazzarelli's misunderstanding of the reproductive system. Mazzarelli (1898) apparently never saw a specimen of *T. perversa.* The only irreconcilable difference between Mazzarelli's specimen and *T. perversa* is the absence of a rachidian row in the former. Ev. Marcus (1985) supposed, probably perfectly correctly, that these very fine teeth had been lost during Mazzarelli's preparation of the radula. When in 1979, Dr. H. Bertsch received another species that was obviously congeneric with *T. duebini,* he consulted Mr. R. Burn and myself over the matter. It was obvious that a new genus was needed. I suggested *Roya* might be suitable by virtue of its conchological, periostracal and radular similarities. However this suggestion was not correct because Marshall (1981) subsequently showed *Roya* to be a basommatophoran pulmonate related to *Siphonaria.* Marshall considered *Roya* as a junior synonym of *Williamia.* Rehder (1984) reiterated Marshall's information. In passing, I must add that Marshall (1981, p.488) erred in stating *R. spongotheras* had a rachidian tooth; he was actually referring to an illustration of *Tylodina fungina.* Since neither *Tylodinella* nor *Roya* can fill the void as a genus for *T. duebini* and *R. spongotheras,* I provide the new name *Anidolyta* (an anagram of the word tylodina with femine termination) for them both with Lovén's species selected as type. Ev. Marcus, to whom I conveyed all the above information during correspondence in 1983, has unintentionally already published the name *Anidolyta* (Ev. Marcus, 1985), but her usage represents a *nomen nudum* being devoid of diagnosis or indication of type species. It was unfortunate her paper appeared before this one of mine.

Anidolyta is the hardest genus in the whole order to delineate fully or separate adequately from other umbraculacean genera because of the lack of comparative anatomical data. Without question it is closest to *Tylodina*, the two being sister groups. *Anidolyta* and *Tylodina* share numerous synapomorphies (already given here under *Tylodina*). Differences between them relate to shell musculature (an intermediate suspensor is present in *Tylodina*), mantle margin (that of *Anidolyta* is crenulate or papillate), rachidian tooth (absent in *Anidolyta*) and denticles on lateral teeth (present in *Anidolyta*). Actually, only the final character can be construed as an autapomorphy for *Anidolyta* with any certainty.

As it is presently conceived, *Anidolyta* is a small genus consisting of two [and possibly a third (Marshall, 1981)] species. They are distinguished primarily by their shells and radular proportions. The shell of *A. duebini* is conical and parallel-sided, and the protoconch is located behind the centre; that of *A. spongotheras* is circular, extremely flattened, and the protoconch is central. There are relatively more teeth in the radula of *A. spongotheras.* Most specimens of these two species have been trawled below 350 m.

Umbraculum Schumacher, 1817

Type species, by monotypy, *Patella umbraculum* Lightfoot, 1786. Recent, cosmopolitan in tropical and warm temperate seas. Fig. 2.

Synonyms: *Patella* Lightfoot, 1786 (non Linnaeus, 1758); *Acado* Lamarck, 1801 (non Commercon, 1792); *Gastroplax* Blainville, 1819; *Umbrella* Lamarck, 1819; *Ombrella* Blainville, 1824; *?Spiricella* Rang, 1827; *Umbrella* Orbigny, 1841; *Operculatum* H. Adams and A. Adams, 1841.

Umbraculum is a unique opisthobranch genus; one that possesses more specialized, derived characters than any other notaspidean. This implies a long separation for *Umbraculum* from the tylodinids, with which it shares an external, patelliform shell and cuticularized labial ring, and even longer separation from the pleurobranchs. *Umbraculum* has undergone considerable reorganization of the body and mantle/gill complex and it has also acquired many autapomorphies, the most significant of which are: flattened shell; voluminous and tough, pustulose foot with deep anterior cleft containing the mouth and non-protrusible penis; two pairs of oral tentacles; lengthening of the gill; broadening of the radula; location of anus posterior to gill basement membrane. No doubt, as more examinations of *Umbraculum* are conducted, more apomorphies will be revealed, e.g. the enormous lengthening of the spermatozoon (Thompson, 1973). The sperm nucleus, which is also very long, is coiled around the axoneme and anterior portion of the mitochondrial derivative. In addition,the centriolar derivative and anterior extension of the mitochondrial derivative are located very close to the axoneme (Healy and Willan, 1984).

Moquin-Tandon's (1870) monograph still stands as the foremost reference source for comparative anatomical detail of *Umbraculum.* Some of the inaccuracies of Moquin-Tandon's description of the reproductive system were corrected by O'Donoghue (1929), Ev. Marcus and Er. Marcus (1967), and Ev. Marcus (1985), but physiological and histological studies are still urgently required to understand the functioning of its complicated reproductive system.

The genus *Umbraculum* is either monotypic as Burn (1959) has suggested (in which case the species should take the earliest available name *Umbraculum umbraculum* Lightfoot, 1786), or bitypic (Thompson, 1970). The literature, right up to the present day, contains a plethora of names most of which are certainly synonyms of *U. umbraculum.*

Pleurobranchus Cuvier, 1804

Type species, by monotypy, *Pleurobranchus peronii* Cuvier, 1804. [Thompson's (1970, p. 179) designation of *Bulla membranacea* Montagu, 1815 as type species is invalid.] Recent, Indo-Pacific Ocean. Fig. 3.

Synonyms: *Oscanius* Gray, 1847; *Susania* Gray, 1857; *Oscaniella* Bergh, 1897.

Pleurobranchs belonging to this long-established genus are relatively large-sized as adults (e.g. *Pleurobranchus grandis* can attain 210 mm) and have apomorphies of tuberculate mantle and gill rachis, cleft anterior mantle border and, in mature adults, flaps surrounding the genital apertures. In addition, the tips of the rhinophores regularly pulsate in living specimens. The large body size, absence of a penial gland and generally simple radular tooth shape point to *Pleurobranchus* as being the least modified genus of the Pleurobranchinae. *Pleurobranchus* is probably nearer to the common ancestor than any genus of the berthelline tribe and hence it shares some characters with *Pleurobranchella*, the genus occupying the same relative position in the Pleurobranchaeinae.

In view of this long history, it is not surprising to note that *Pleurobranchus* possesses a relatively large number of characters showing apomorphic traits (i.e. shell sometimes absent, shell size, shell location, mantle to shell ratio, single denticle at base of some radular teeth, one or two allosperm receptacles, prostate gland condition). Because it seems to be a large genus numerically, authors have attempted to split *Pleurobranchus* (presumably on the assumption that it was paraphyletic) by creating or recognizing genera based on one or a few of these apomorphic traits. Such attempts have been unsuccessful because these traits do not occur concordantly, and I agree with Thompson (1970) and Baba and Hamatani (1971) in recognizing only *Pleurobranchus. Oscanius* is the first of three such sometime recognized genera; its characters being the shallow anterior mantle notch, single denticle on blade of mandibular element, large and thin (uncalcified) shell, innermost lateral radular teeth with a basal denticle (Burn, 1962). However outgroup comparison (with the Berthellini) shows several species there that possess identical character states. Neither has *Oscanius* a single apomorphy; so it cannot be separated, even as a subgenus, from *Pleurobranchus. Susania* in another such genus; its characters being the thick mantle, deep anterior mantle notch, several denticles on blade of mandibular element, shell absent or present (in which case it is very small, oval, calcareous and located posteriorly) (Burn, 1962). The only apomorphies possessed by *Susania* are the greatly thickened mantle and small shell. *Oscaniella* is the third such genus; its characters being the relatively small mantle tubercles, small, anteriorly-located shell and lack of flaps surrounding the genital aperture (Bergh, 1897, 1905). The final character is erroneous - probably Bergh's animals were immature. The other two characters are either possessed by other species of *Pleurobranchus* or are homeoplasies of other pleurobranchine species. Recognition of *Oscanius, Susania* or *Oscaniella* as genera or subgenera, based solely on one character (out of all of these given above), is completely unjustified.

In an earlier paper (Willan, 1983), I was equivocal about the status of *Pleurobranchus* and its relationship to *Berthella,* reflecting the uncertainty in the existing literature. It is now clear that both *Pleurobranchus* and *Berthella* are distinct genera and not particularly closely related, their shared character states being symplesiomorphies or homeoplasies.

Pleurobranchus species have wide distribution ranges in tropical waters of the Mediterranean, Indian, Pacific and Atlantic Oceans. The apparent absence or rarity of *Pleurobranchus* species from the coral atolls of the central Pacific region (Willan, 1984b) is inexplicable at present. Diversity of *Pleurobranchus* species decreases rapidly in temperate waters where, in general, they are replaced (phylogenetically not ecologically) by *Berthella* species.

Berthella Blainville, 1825

Type species, by original designation, *Berthella porosa* Blainville, 1825 (= *Bulla plumula* Montagu, 1803). Recent, North Atlantic Ocean. Fig. 4.

Synonyms: *Cleanthus* Gray, 1847; Bouvieria Vayssière, 1896; *Gymnotoplax* Pilsbry, 1896; *Berthellinops* Burn, 1962.

The genus *Berthella* has unfortunately had a tortuous taxonomic history because it was confused with *Berthellina* (Gardiner, 1936; Odhner, 1939). Its generic nomenclature is now settled. Willan (1978) examined the holotype of *Gymnotoplax americanus* Verrill and showed that it was a species of *Berthella* with the mantle mutilated to such a degree the shell had become uncovered.

It is probable that *Berthella* formed the stock from which other Recent genera of the tribe in Berthellini evolved—*Bathyberthella, Pleurehdera* and *Berthellina.* In *Berthella* there is a pool of characters showing apomorphic traits. Several of these traits also occur in other pleurobranchine genera, for example the relatively large shell (covering the whole of the viscera), a denticle at the base of some of the lateral teeth, smooth blades to the mandibular elements, reduction of the number of allosperm receptacles to one and a distinct prostate gland. Others are unique to *Berthella* i.e. mantle autotomy and anal site in front of the middle of the gill's suspensory membrane. Like *Pleurobranchus, Berthella* appears to have had a long evolutionary history, but unlike *Pleurobranchus,* malacologists have not attempted to split *Berthella* into other genera. When the anatomy of more species is known, a division into subgenera may be possible. Characters that should repay further attention in this context are the mantle (i.e. spicules, fine structure of epithelial and sub-epithelial glands), anal position, reproductive system, autotomy and feeding behavior.

Berthella is a moderately large genus with its constituent species widespread geographically and bathymetrically. Several species are common in the intertidal and shallow subtidal zones where they play a significant role in structuring encrusting communities by grazing sponges (Cattaneo, 1982; Willan, 1984a; Willan and Morton, 1984).

Bathyberthella Willan, 1983

Type species, by original designation, *Bathyberthella* *zelandiae* Willan, 1983. Recent, New Zealand.

Bathyberthella is the most recently characterized pleurobranch genus. Rather than being erected to contain a number of existing species, *Bathyberthella* was created to accommodate initially one (now two) newly described species from deep water. Its external features resemble those of *Berthella, Berthellina* and *Pleurehdera* and many of its characters, both external and internal, are symplesiomorphies shared with those three genera, i.e. smooth non-emarginate mantle, smooth gill rachis, simple radular teeth, prostatic dilation of vas deferens, triaulic reproductive system. However, *Bathyberthella* does possess four important, internal apomorphies: a very large, flexible, cuticular shell; long; tubular median buccal gland (that is apparently not branched distally); narrow, erect radular teeth; narrow, oval or elliptical mandibular elements that lack lateral processes and have an irregularly denticulate anterior margin. One species of *Pleurobranchus, P. membranaceus,* also possesses an uncalcified cuticular shell. That homeoplaseous state must have, therefore, occurred congruently in the two genera; occurring as an apomorphy in *Bathyberthella* and an apomorphic trait in *Pleurobranchus.* In the phylogenetic analysis (Fig. 20), no apomorphy could be found to link *Bathyberthella* more closely to either the *Berthella* branch or the *Berthellina/Pleurehdera* branch. In the strictly dichotomous dendrogram (Fig. 21), *Bathyberthella* was located as a sister group to *Berthella.*

The "unexpected amalgam of characters" (Willan, 1983) possessed by *Bathyberthella* are the reasons for the slight differences in its placing between the cladogram and dendrogram. Indeed, *Bathyberthella* is a most signigicant genus. The form of its mandibular elements is highly important and difficult to explain. Its mandibular elements are narrow and oval (i.e. of the polygonal type) with denticulate anterior margins. Previously, I had interpreted the form of these elements as indicative of a relationship with the Pleurobranchaeinae (Willan, 1983), but it is now apparent that the affinities of *Bathyberthella* lie wholly with the genera of the Pleurobranchinae, and in particular, the tribe Berthellini (Willan and Bertsch, 1987). One symplesiomorphy of this subfamily is possession of mandibular elements of the cruciform type (present in every species of all the other four genera), so the occurrence of the polygonal ones mentioned above in *Bathyberthella* is most unexpected. There are two opposing hypotheses to account for the presence of polygonal elements. Either *Bathyberthella* represents the termination of a lineage that stemmed independently from the very base of the Pleurobranchinae (i.e. its mandibular elements retain the plesiomorphic, ancestral state) or it has lost the cruciform elements of others of its tribe and acquired new ones anatomically convergent with those of the ancestor. I favoured the former hypothesis because it was more parsimonious when describing *Bathyberthella,* but have subsequently rejected it because all the other characters tie *Bathyberthella* so firmly with the rest of the tribe Berthellini.

The two species of *Bathyberthella* are allopatric. Each apparently occupies a restricted geographic range and each possesses apomorphies of its own. *B. zelandiae* occurs below 1600 m on the Bounty Trough, southwest of New Zealand. It has an enlarged buccal mass that can be protruded for up to half the body length, large eyes (unusual for an abyssal mollusc), 4-14 denticles (mean = 10.14) on the anterior border of the mandibular elements, and minute papillae on the rhinophores and oral veil (Willan, 1983). *B. antarctica* is known from 128 to 486 m in waters bordering the Antarctic continent. It's apomorphies are large size (specimens are approximately 120 mm long when adult, making it easily the largest member of the Berthellini); disproportionate enlargement of the foot with respect to the mantle; subterminal site of the protoconch with respect to the teleconch; very long median buccal gland, 1 to 5 denticles (mean 3.25) on the anterior border of the narrow mandibular elements; enlargement of the ovotestis; loss of penial gland (Willan and Bertsch, 1987). Probably these apomorphies represent adaptations by *B. antarctica* to the Antarctic environment.

Pleurehdera Er. Marcus and Ev. Marcus, 1970
Type species, by original designation, *Pleurehdera haraldi* Er. Marcus and Ev. Marcus, 1970. Recent, Tuamoto Archipelago, Pacific Ocean. Fig. 5.

Pleurehdera is the most weakly characterized of any of the tribe Berthellini and it is very close to *Berthellina.* Its sole character that could be held up as an apomorphy is the greatly enlarged pedal gland that is supposed to take up almost half the foot sole and occupy the full width of this posterior section (Er. Marcus and Ev. Marcus, 1970). It is important however to note that a later investigation of new material failed to reveal any such gland (Willan, 1984b), so its presence in the unique holotype might have been an artifact of preservation. Even so, *Pleurehdera* shows no relationships with *Pleurobranchus* as claimed by Er. Marcus and Ev. Marcus (1970) on the pedal gland alone, since this gland is now known to be present in sexually mature individuals of many species of the subfamily Pleurobranchine. Characters separating *Pleurehdera* from *Berthellina* are the relatively larger shell and low point of origin of the receptaculum seminis off the vagina in *Pleurehdera* (both character states occur elsewhere in the Berthellini), and form of the radula. In *Pleurehdera*, the teeth are elongate, the innermost laterals possess a single denticle at their base and middle laterals posses a denticle near the cusp (Er. Marcus and Ev. Marcus, 1970; Willan, 1984b).

Pleurehdera is a monotypic genus. *P. haraldi* probably occurs throughout the tropical, central Pacific Ocean. Its known depth range is from 3 to 12 m. Willan (1984b) has redescribed *P. haraldi* on the basis of material from the Marshall Islands.

Berthellina Gardiner, 1936
Type species, by original designation, *Berthellina engeli* Gardiner, 1936. Recent, North Atlantic Ocean. Fig. 6.
Synonym: *Berthella* Vayssière, 1896 (non Blainville, 1825).

The distinctive lamellate shape of the radular teeth (very elongate with numerous denticles on the posterior face of the distal half of the blade) is the major autapomorphy possessed by species of this genus. The pedal gland has been lost. Apomorphic traits are for a small and spatulate shell (or none at all), for the shell to be located centrally or anteriorly above the viscera, for the anterior mantle margin to be entire or weakly emarginate, and for the blades of the mandibular elements to be smooth or very weakly denticulate. In attaining only small adult size and possessing a smooth mantle and gill rachis, species of *Berthellina* are indistinguishable in body form externally from species of the other three genera of the tribe Berthellini.

Berthellina is not a speciose genus, there being fewer than six valid species. However the genus is well known because some of its constituent species are widespread geographically (e.g. *Berthellina citrina*) and rather common. All species occur in tropical and warm temperate waters and they range from the intertidal zone to moderate subtidal depths.

Pleurobranchella Thiele, 1925

Type species, by monotypy, *Pleurobranchella nicobarica* Thiele, 1925. Recent, Indian Ocean.

Synonyms: *Pleurobranchoides* O'Donoghue, 1929; *Gigantonotum* Guangyu and Si, 1965.

Anatomical data are gradually being accumulated on this interesting genus. Such data have been unavailable in the past because of paucity of material. O'Donoghue's (1929) account of *Pleurobranchoides gilchristi* is the most complete of any of the descriptions of new species. Er. Marcus and Ev. Marcus (1970) first mentioned the similarity of *Pleurobranchoides* to *Pleurobranchella*. Willan (1977) synonymized both genera as well as *Gigantonotum*. Ev. Marcus and Gosliner (1984) regarded *Pleurobranchella* as monotypic but preferred to consider *Gigantonotum* as "a distinct but doubtful genus" on the ground that its reproductive system had not been described.

Willan (1977) has already presented a definition of *Pleurobranchella*. It is important, at this time, to separate the plesiomorphies from the apomorphies contained in that definition. Several of the characters of *Pleurobranchella* represent plesiomorphies for the subfamily Pleurobranchaeinae (and in fact the family Pleurobranchidae too); these are: the very large mantle that covers the foot laterally and posteriorly; simple radular teeth; polygonal mandibular elements with denticulate anterior edges; diaulic reproductive condition; two allosperm receptacles. Most of these characters are also plesiomorphies for the *Pleurobranchella - Pleurobranchaea* lineage. On the other hand *Pleurobranchella* does possess three apomorphies for the *Pleurobranchella-Pleurobranchaea* lineage: tuberculate mantle; broadly expanded oral veil; muscle penial sac accommodating coils of the distal vas deferens. Finally *Pleurobranchella* possesses four apomorphies of its own: loss of pedal gland; tuberculate gill rachis; distinct prostate gland; penial papillae. However, the latter three specializations are apparently only possessed by some species (i.e. they are apomorphic traits). Outgroup comparison reveals not one of these four apomorphies to be unique to *Pleurobranchella:* the pedal gland has also been lost independently in *Berthellina; Pleurobranchus* also has a tuberculate gill rachis; *Umbraculum* also has a distinct prostate gland; *Euselenops* has penial papillae. Because *Pleurobranchella* retains so many primitive characters and so few unique derived ones, Willan (1977) hypothesized that it was closer to the ancestor of the pleurobranchaeine stem than either *Pleurobranchaea* (its sister group) or *Euselenops*. Nothing revealed in this study has altered that opinion. Thus *Pleurobranchella* is specially significant because it is the most primitive extant genus in the most advanced pleurobranch subfamily. There is every reason to believe *Pleurobranchella* represents a relict genus.

There are probably less than four biological species of *Pleurobranchella* worldwide. Indeed, as Ev. Marcus and Gosliner (1984) indicated, the genus may be monotypic. The genus is widespread in the tropical Indian and western Pacific Oceans. All material has come from depths greater than 200 m. Natural diet is unknown, but there is one record of predation on juvenile *Pleurobranchaea* (Eales, 1937).

Pleurobranchaea Meckel in Leue, 1813

Type species, by subsequent monotypy (Blainville, 1825, p. 376), *Pleurobranchidium meckelii* Blainville, 1825. Recent, Mediterranean Sea. Fig. 7.

Synonyms: *Pleurobranchidium* Blainville, 1825; *Cyanogaster* Blainville 1825; *Koonsia* Verrill, 1882; *Pleurobranchillus* Bergh, 1892; *Macfarlandaea* Ev. Marcus and Gosliner, 1984 (syn. nov.).

Pleurobranchaea and *Pleurobranchella* represent sister groups with *Pleurobranchaea* the more speciose and variable. Unfortunately many of its nominal species are insufficiently described (Er. Marcus and Ev. Marcus, 1966; Willan and Bertsch, 1987), and this lack of comparative data hampered my tabulation of character states for this genus. Now that species of *Pleurobranchaea* are regularly used in neurophysiological research (e.g. Davis, 1975; Siegler, 1977a, b; McClelland, 1983), nontaxonomists should be aware that much of the literature on *Pleurobranchaea* is burdened under a plethora of unrecognizable synonyms. Future descriptions of novel species and appraisals of existing ones must take ontogenetic and intraspecific variation into account. No additional species should be based an holotype that is immature.

Gosliner (1985) has recently reiterated the propositon that *Koonsia* is a junior synonym of *Pleurobranchaea* (Willan, 1977, 1983). Besides being taxonomically unnecessary, the recently described taxon *Macfarlandaea* is unsound because both (the only two) characters used to define it (Ev. Marcus and Gosliner, 1984, p. 40) are wrong (i.e. not possessed by the type species). Contrary to Ev. Marcus and Gosliner's definition that *Macfarlandaea* has "rudimentary secondary cusps on all radular teeth", MacFarland (1966, p. 90, pl. 15, figs. 16, 17, 21) clearly indicated their absence, in *P. californica,* from the first row of laterals as well as from several of the outermost rows of lateral teeth. The statement "Pleurembolic penis with cuticular stylet" is also invalidated by MacFarland's account of *P. californica* (MacFarland, 1966, p. 99, pl. 17, figs. 1, 2); the penis of that species is actually muscular and filiform, and there is no stylet whatsoever.

Two characters appear for the first time (as apomorphic traits) in *Pleurobranchaea*, posterior fusion of the mantle and foot, and a caudal spur on the upper surface of the tail. The median buccal gland is enlarged in *Pleurobranchaea* so that its network of tubules extends between all the organs at the front of the visceral cavity (Willan, 1975; Morse, 1984). All species of *Pleurobranchaea* have reduced the size of the mantle. Other apomorphies are difficult to find; I think this is not because they do not exist (*Pleurobranchaea* is undoubtedly holophyletic), but because they have not been looked for. For example, initial investigations into the ultrastructure of its sperm revealed a very short glycogen piece that was devoid of any axonemal remmant (Healy and Willan, 1984).

Species of *Pleurobranchaea* occur in temperate waters in both hemispheres. In view of this wide distribution and relative abundance of certain species, it is surprising that so little is known conclusively of the natural diet. The only generalizations that can be made are that *Pleurobranchaea* species are active, opportunistic carnivores eating whole soft-bodied invertebrates or scavengers, and that cnidarians are amongst the more preferred food items (Willan, 1984a).

Euselenops Pilsbry, 1896
Type species, by monotypy, *Pleurobranchus luniceps* Cuvier, 1817. Recent, Indo-Pacific Ocean. Fig. 8.
Synonyms: *Neda* H. Adams and A. Adams, 1854 (non Mulsant, 1851); *Oscaniopsis* Bergh, 1897.

The genus is monotypic with its sole species, *Euselenops luniceps,* being widely distributed throughout the Indo-Pacific Ocean. Because of this extensive range and accessibility (*E. luniceps* occurs relatively abundantly in moderately shallow water), sufficient specimens have been collected to allow its anatomy to be described thoroughly (e.g. Bergh, 1897; Vayssière, 1901; O'Donoghue, 1929; Guangyu and Si, 1965; Thompson, 1970). In addition, its intraspecific variability is now understood and this has proved not to be great.

The external features of *Euselenops luniceps* are so distinctive that it was segregated into a subgenus distinct from *Pleurobranchaea* in the first synthesis of the Notaspidea (Pilsbry, 1896); this was even before its internal anatomy was known. Detailed anatomical studies laid even greater emphasis on its external diagnostic characteristics (Bergh, 1897; Vayssière, 1901), and *E. luniceps* was soon placed in a genus of its own. No malacologist has challenged this generic placement subsequently. Actually, the most notable apomorphies of *Euselenops* are external, i.e. the reduction of the mantle, the permanent mid-posterior mantle crenulation, the enlargement and increased flexibility of the foot, the enormous enlargement of the oral veil. All these apomorphies are probably related to the newly assumed habit of shallow burrowing, a behavior never displayed by other pleurobranchaeines. The mantle's smoothness is, by contrast, a plesiomorphy for this subfamily. The internal systems of *Euselenops*, particularly the alimentary and reproductive systems, are relatively conservative with the majority of characters showing the plesiomorphic state for the subfamily, e.g. the relatively small median buccal gland, simple radular teeth, absence of coiling of vas deferens within a penial sac. However, the presence of many papillae on the penis undoubtedly represents one internal apomorphy. O'Donoghue (1929) described the nervous system as being distinct from all other genera in the Pleurobranchidae.

Euselenops luniceps appears to be the most advanced member of the Pleurobranchidae. It certainly represents the culmination of pleurobranch evolution as regards behavioral sophistication; it is highly active and carnivorous, and it can swim. Unfortunately we are completely ignorant of its diet (Willan, 1984a). Therefore studies on feeding and breeding behavior are urgently needed for *E. luniceps.*

CONCLUSION

The purpose of this investigation has been a consideration of phylogenetic relationships within the notaspidean opisthobranchs. This study has, by application of Hennigian methodology, generated a phylogenetic hypothesis. Confirmation for this hypothesis came from computer analysis. Once anatomical data is available, it should be possible to explore relationships between the Notaspidea and other groups of opisthobranch gastropods more thoroughly. Again, the Hennigian approach should prove enlightening.

The hypothesis presented in this paper advocates a monophyletic origin for the Notaspidea. Significant characters uniting all members are the longitudinally-slit rhinophores (obviously derived from the cephalaspidean head shield); broad velar connection between the oral tentacles, lateral bipinnate gill, and anal site at the rear of the gill. A fundamental division soon split the notaspidean stock and the resulting divergent evolution, with concomittant trends of shell reduction and re-establishment of bilateral symmetry, produced the umbraculaceans and the pleurobranchaceans. The umbraculaceans dichotomized again to result in the conservative Tylodinidae and the peculiarly specialized Umbraculidae whilst the pleurobranchaceans maintained their homogeneity. The considerable set of pleurobranchacean apomorphies is proof of that group's monophyly. Major pleurobranchacean evolutionary trends are for shell reduction, fusion of mantle with head (anteriorly) and tail (posteriorly), and dietary radiation. Although there are good reasons to support Minichev's (1970) contention that the Nudibranchia is paraphyletic, there being two fundamentally different groups, the Anthobranchia (= Doridacea) and Cladobranchia (= Dendronotacea, Arminacea and Aeolidacea), I seriously doubt his arguments in favour of evolution of one or both these nudibranchiate groups from notaspideans. Some basic relationships do exist between notaspideans and anthobranchs, symplesiomorphies being details of gill ennervation, joint existance of visceral "blood glands", similar circulatory systems, ptenoglossan radulae, two jaws, lack of branching of digestive gland, sponge diet and possession of two allosperm receptacles. Both groups probably evolved from the same cephalaspidean group simultaneously. However, because each group has subsequently acquired so many specialized derived characters I see no advantage in lumping them together into one order. The origins of the cladobranchs are still more vexing; they most certainly cannot be derived from "higher notaspideans" as Minichev suggested.

This study of the order Notaspidea has presented one hypothesis for its evolution. It now only remains to translate that hypothesis into a taxonomic (= Linnaean) hierachy (Table 6). In fact, this hypothesis generally supports the classification that already exists (Table 1). The fundamental notaspidean divisions are best recognized as suborders. Within the Umbraculacea is a sole superfamily, Tylodinoidea[1], with two families, Tylodinidae (containing two genera) and Umbraculidae (containing only one genus). Within the Pleurobranchacea is one superfamily, Pleurobranchoidea, and family, Pleurobranchidae, with two subfamilies, Pleurobranchinae (containing five genera) and Pleurobranchaeinae (containing three genera). Two tribes, Pleurobranchini (containing only *Pleurobranchus*) and Berthellini (containing *Berthella, Bathyberthella, Pleurehdera* and *Berthellina*), warrant separate recognition within the subfamily Pleurobranchinae.

Table 6. Revised higher classification of the Notaspidea.

- Order Notaspidea Fischer, 1883
  - Suborder Umbraculacea Dall, 1889
    - Superfamily Umbraculoidea Dall, 1889
      - Family Tylodinidae Gray, 1847
        - Genus *Tylodina* Rafinesque, 1819
        - Genus *Anidolyta* Willan, nov.
      - Family Umbraculidae Dall, 1889
        - Genus *Umbraculum* Schumacher, 1817
  - Suborder Pleurobranchacea Férussac, 1822
    - Superfamily Pleurobranchoidea Férussac, 1822
      - Family Pleurobranchidae Férussac, 1822
        - Subfamily Pleurobranchinae Férussac, 1822
          - Tribe Pleurobranchini Férussac, 1822
            - Genus *Pleurobranchus* Cuvier, 1805
          - Tribe Berthellini Burn, 1962
            - Genus *Berthella* Blainville, 1825
            - Genus *Bathyberthella* Willan, 1983
            - Genus *Pleurehdera* Ev. Marcus and Er. Marcus, 1970
            - Genus *Berthellina* Gardiner, 1936
        - Subfamily Pleurobranchaeinae Pilsbry, 1896
          - Genus *Pleurobranchella* Thiele, 1925
          - Genus *Pleurobranchaea* Meckel in Leue, 1813
          - Genus *Euselenops* Pilsbry, 1896

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[1] Terminations for superfamilies and tribes follow Recommendation 29A of the most recent edition of the International Code of Zoological Nomenclature (I.C.Z.N. 1985).

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BIOGEOGRAPHY OF THE OPISTHOBRANCH GASTROPOD FAUNA OF SOUTHERN AFRICA

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ABSTRACT

In temperate Atlantic and Indian Ocean waters of southern Africa, endemic and Atlantic opisthobranch mollusks are predominant, while in tropical waters of the region these are replaced by Indo-Pacific and circumtropical species. Well-defined boundaries, previously described for southern African biogeographical provinces, are blurred when opisthobranchs are considered. However, distinct temperate and tropical faunas are present. Most of the Indo-Pacific species present in southern Africa extend well across the Indian Ocean, and a majority of species are also found on the non-marginal portions of the Pacific Plate.

Sister group relationships suggest that the southern African opisthobranch fauna is phylogenetically and biogeographically linked to three primary regions: sub-Antarctic, North Atlantic and Indo-Pacific. Links with sub-Antarctic species appear to be the oldest and may be related to cold water present during the Pliocene. Relationships with North Atlantic species are more recent (Pleistocene) and also appear to be related to major oceanographic and climatic changes.

Levels of endemism between opisthobranch and prosobranch gastropods differ and appear to be related to differing life history strategies. Contrary to the view of some authors, that large discrepancies in levels of endemism in different taxa are simply systematic artifacts, these discrepancies could actually represent challenges to simplistic vicariant hypotheses. The notion that sister species relationships of endemic species provide the only meaningful biogeographical data is discussed and challenged.

Southern Africa represents a region that is crucial to the understanding of marine biogeography. The convergence of the Atlantic and Indian Oceans, characterized by water masses of divergent physical oceanographic characteristics, accentuates the geographical importance of this region. This variation of temperature regimes and oceanic currents supports a rich marine biota with phylogenetic and biogeographical links to species in other southern oceans, the northern Atlantic and the Indo-Pacific trophics.

Previous studies on the distribution of the marine biota of southern Africa have been largely descriptive and have attempted to characterize the species composition of the region and to delimit biogeographical provinces (Ekman, 1953; Macnae and Kalk, 1958; Day, 1967; Briggs, 1974; Griffiths, 1974; Brown and Jarman, 1978; Millard, 1978; Kensley, 1981, 1983; Kilburn and Rippey, 1982). An excellent description of the biological and physical oceanographic characteristics of the region was provided by Brown and Jarman (1978) and will not be repeated here.

Vicariance biogeographical theory (Croizat, 1958; Croizat *et al.,* 1974; Nelson, 1978; Nelson and Platnick, 1981; Springer, 1982) provides additional historical perspectives and suggests causes of geographical isolation that must also be taken into consideration.

Most opisthobranch gastropods have planktonic veliger larvae, which are induced to metamorphose from a pelagic to a benthic existence by the presence of an environmental cue, generally a specific biochemical product produced by the adult food source (Hadfield and Karlson, 1969; Harris, 1975; Switzer-Dunlap and Hadfield, 1977; Bonar, 1978). In the absence of this cue, larvae of many species can delay metamorphosis for variable periods and continue to filter-feed in the plankton until the cue is present, or until they lose their viability and die. This plasticity provides a potential for gastropod larvae to be transported long distances by oceanic currents and, in some cases, to cross entire ocean basins (Scheltema, 1971a, b, 1972; Kempf, 1981). Direct development, in which the larva undergoes its entire

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embryonic and larval development within a benthic egg capsule and is never planktonic, is rare in opisthobranch gastropods and has been reported in about a dozen species (Hadfield, 1963; Bridges, 1975; Bonar, 1978; Gosliner and Griffiths, 1981; Rose, 1985). Prosobranch gastropods exhibit the same range of developmental modes that opisthobranchs do, but direct development and short-term planktonic development are the dominant patterns in many taxa (Fretter and Graham, 1962; Morton, 1968; Webber, 1977). Scheltema and Williams (1983) have suggested that closely related marine organisms with differing life-history modes can have different distributional patterns that are directly related to their relative dispersal capabilities. One might expect that opisthobranchs, with few species having direct or short-term development, would exhibit less endemism and more widespread distributions than do prosobranch gastropods.

This paper examines the distribution patterns exhibited by opisthobranch gastropods in southern Africa and compares them with those described previously for other marine taxa. The universality of biogeographical boundaries within the region is discussed. The relative importance of possible vicariant events and subsequent dispersal in the evolution of the opisthobranch fauna of southern Africa is considered. The relevance of differences in levels of endemism as an indicator of the validity and applicability of vicariant hypotheses is discussed.

METHODS

SOURCES OF DATA

The Opisthobranchia studied here include representatives of all the major benthic orders of the subclass. Members of the Pyramidellidae have been recently excluded from the Opisthobranchia (Gosliner, 1981a), and are excluded from this study. The holoplanktonic Thecosomata and Gymnosomata are poorly documented from southern African waters and are not included in the present examination. No members of the Acochlidiacea have been recorded from southern Africa.

At first appearance, the opisthobranch fauna of southern Africa appears to be well studied (Linnaeus, 1767; Quoy and Gaimard, 1823; Rang, 1828; Krauss, 1848; Stimpson, 1854; Gould, 1859; Sowerby, 1873, 1892, 1894, 1897; Martens, 1879; Watson, 1886; Pelseneer, 1888; Gilchrist, 1900; Vayssière, 1900; Smith, 1902, 1903, 1910; Eliot, 1905, 1910; Meisenheimer, 1905; Bergh, 1907; Thiele, 1912, 1925; Bartsch, 1915; Tomlin, 1920; Barnard, 1927, 1932, 1933, 1934, 1963a, b; O'Donoghue, 1929; Turton, 1932; Macnae, 1954a, b, 1955, 1957, 1958, 1962a, b; Macnae and Kalk, 1958; Thompson, 1979; Thompson and Brown, 1981; Gosliner, 1981b, 1982, 1985; Gosliner and Griffiths, 1981; Ev. Marcus and Gosliner, 1985; Millen and Gosliner, 1984; Gosliner, 1985; Griffiths, 1985). Approximately 209 species of opisthobranchs from South Africa and Mozambique have been recorded. I conducted field observations spanning a three year period from November 1979 to November 1982, and in May 1984 along much of the southern African coast from Lamberts Bay on the Atlantic coast to Kosi Bay on the South African-Mozambique border. Material was collected from the intertidal zone and the subtidal zone. Subtidal collections were made by means of scuba diving to a depth of 40 m and by trawling and dredging to a depth of 90 m. These investigations yielded specimens of 190 species of opisthobranchs not previously recorded from southern Africa, including 120 undescribed species. Although a large percentage of species within southern Africa is undescribed, reliable distributional data from a wide geographical area are available for many of them. Previously unpublished distributional data for these species are included in the analysis presented here.

Other unpublished records of opisthobranch mollusks have also been incorporated in this study. These include collections from Madagascar, Reunion Island and Tanzania by Michael Gosliner and Gary Williams, my own data collected from the Seychelles and Hawaiian Islands and material from the collections of the Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

DEFINITIONS

Southern Africa, for the purposes of this study, includes the region south of 15° S latitude, from Mocamedes, Angola, on the Atlantic coast, to Mozambique Island in the Indian Ocean. Employing these limits is expedient for two reasons: most other studies of the faunas of southern Africa are restricted to these geographical limits (Barnard, 1950; Kensley, 1981), and few data are available for the areas immediately to the north of these limits.

Many terms used in biogeographical studies have ambiguous meanings and have been the cause of misinterpretation. For this reason, their specific applicability to the scope of this paper is explained. The term endemic, in the present context, applies to species that are believed to be restricted to southern Africa. Circumtropical species are here defined as those recorded from at least some portion of each of the tropical Atlantic, Indian and Pacific Oceans. Indo-Pacific species are those recorded from at least some portion of the tropical Indian and Pacific Oceans, but not from the Atlantic Ocean. Indo-West Pacific species, following Springer (1982), are differentiated from Indo-Pacific species by being present throughout the Indian Ocean, but only in the western margin of the Pacific Plate. Cosmopolitan species are regarded as being widespread, not limited to tropical or temperate regions. Atlantic species are those found in some portion of the Atlantic Ocean aside from the coast of southern Africa.

For the purposes of this study, species are placed in the broadest applicable geographic classification. For example, a species found in South Africa, East Africa, the Hawaiian Islands and Brazil would be considered to have a circumtropical distribution.

SELECTION OF GEOGRAPHICAL SITES

Virtually all previous workers who have studied the marine biota of southern Africa have concluded that there are several distinct biogeographical provinces within the region (see Brown and Jarman, 1978; Kensley, 1981; Kilburn and Rippey, 1982), with varying degrees of overlap between them. It is, therefore, less informative to present distributional

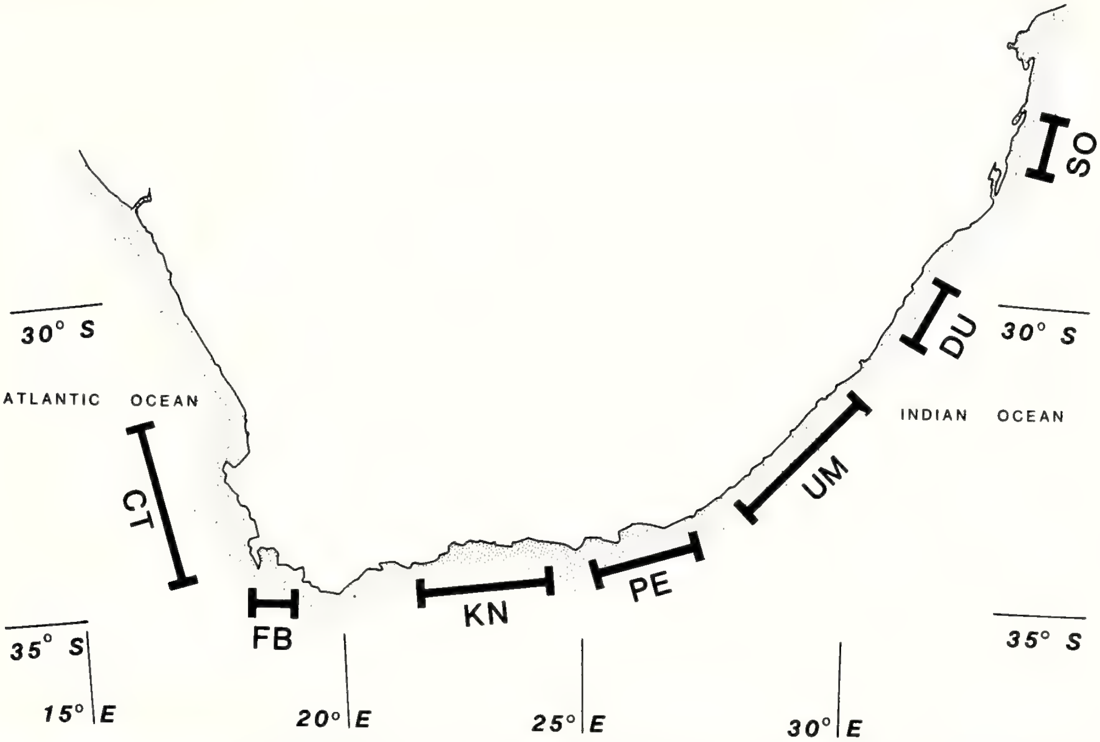

Fig. 1. Geographical regions examined in this study (CT - Cape Town, FB - False Bay, KN - Knysna, PE - Port Elizabeth, UM - Umgazana, DU - Durban, SO - Sodwana Bay).

data for the entire region as a single fauna. Rather, it is appropriate to define different geographical areas in order that their biogeographical affinities may be contrasted. Seven areas (Fig. 1) were selected in order that comparisons can be made. They represent most of the previously described variation in oceanographic conditions and include the geographic extent of the region. In addition, these areas were selected because they have been reasonably well studied and are likely to reflect an accurate sample of the total opisthobranch fauna of the region. The areas chosen are centered at Cape Town (Lamberts Bay to Cape Point), False Bay (Buffle's Bay to Rooi Els), Knysna (Still Bay to Storm's River Mouth), Port Elizabeth (Jeffreys Bay to Port Alfred), Umgazana (Gonubie to Port St. Johns), Durban (Park Rynie to Salt Rock) and Sodwana Bay (Adlam's Reef to Kosi Bay). The localities in parentheses represent the geographical limits of each area considered. Not all areas are of equal size nor have they been sampled with equal intensity. For example, virtually no sublittoral samples have been collected from Umgazana. Despite these potential biases, several distinct patterns emerge.

RESULTS

Distributional data within southern Africa and outside the region are presented for 237 species of opisthobranchs (Appendix 1). The percentages of endemic, circumtropical, Indo-Pacific, Atlantic and cosmopolitan species present in each of the seven regions are compared (Fig. 2). Several obvious trends emerge when these data are compared. There is a high incidence of endemism in the southwestern portion of southern Africa, which abruptly diminishes in the localities to the east of Port Elizabeth. There is also a small percentage of Indo-Pacific and circumtropical species present in the southwestern portion of southern Africa, which increases markedly in an eastward direction. A significant number of Atlantic species is found in the southwestern and southeastern portions of the Cape Province but these are notably absent from Transkei and Natal localities.

Even more significant is the abrupt faunal shift in the geographical affinities between Port Elizabeth and Umgazana. In Cape Town, False Bay, Knysna and Port Elizabeth the majority of species are endemic or Atlantic. In Umgazana, Durban and Sodwana Bay most species are circumtropical or Indo-Pacific.

DISCUSSION

FACTORS THAT AFFECT BIOGEOGRAPHICAL CONCLUSIONS

Biogeographical studies are limited by the level of knowledge of the geographical area of immediate concern, and by the available data from adjacent or associated regions. This is certainly true of the opisthobranch fauna of southern Africa.

Relatively few studies have been conducted on the opisthobranch faunas of the west coast of Africa. Ev. Marcus and Er. Marcus (1966, 1968) recorded 19 species of

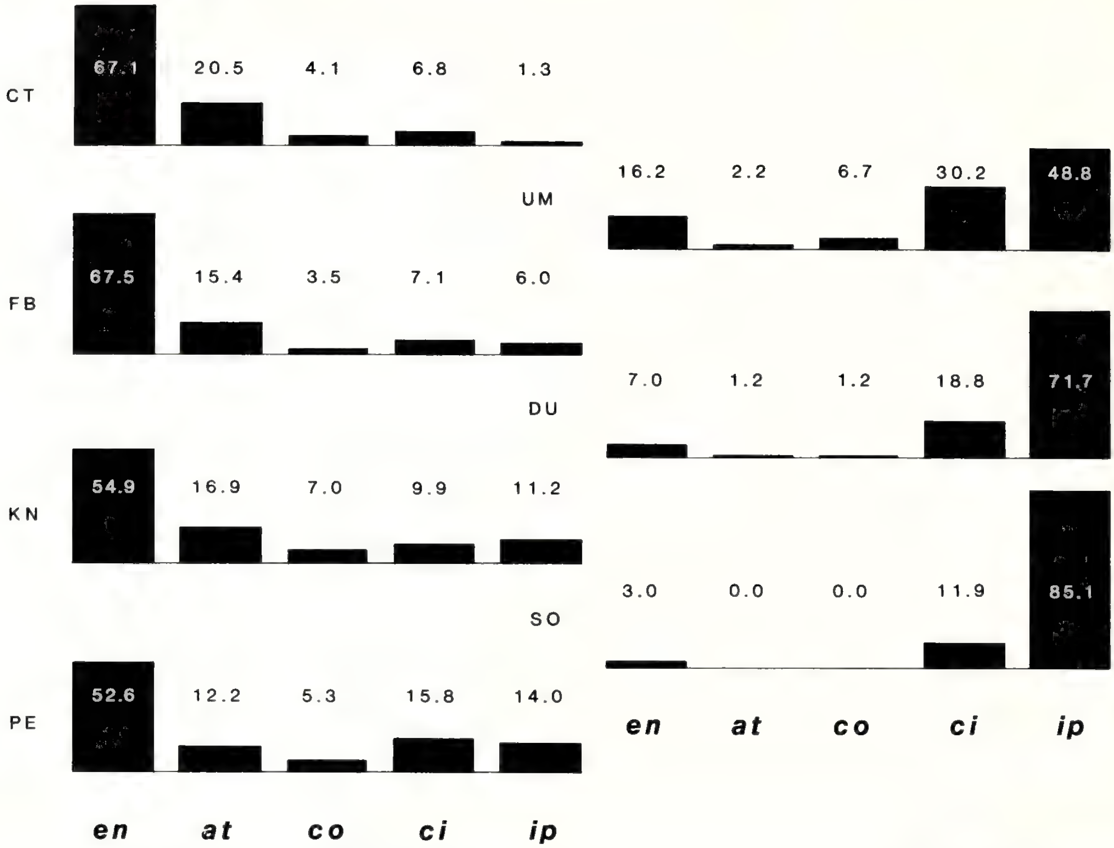

Fig. 2. Biogeographical affinities of southern African opisthobranchs within the seven regions studied (CT - Cape Town, FB - False Bay, KN - Knysna, PE - Port Elizabeth, UM - Umgazana, DU - Durban, SO - Sodwana Bay, en - endemic, at - Altantic, co - cosmopolitan, ci - circumtropical, ip - Indo-Pacific).

opisthobranchs from the Gulf of Guinea and six species from the Ivory Coast. Edmunds (1977, 1981) conducted the most comprehensive studies of West African opisthobranchs and recorded 46 species from Ghana. The only other locality that has been studied is Senegal, from which Pruvot-Fol (1953) recorded 11 species and Bouchet (1971) listed an additional three species.

Most of the coast of East Africa and the islands of Madagascar and Reunion have been poorly studied. Twenty-six species of opisthobranchs have been reported from Madagascar (Ev. Marcus and Er. Marcus, 1970), fourteen species from the Seychelles (Edmunds, 1972) and 35 species from Mauritius (Bergh, 1888, 1889). The portion of East Africa that has been most thoroughly investigated is the coast of Tanzania, including Zanzibar (Eliot, 1902, 1903a, b, 1904a, b, c; Edmunds, 1969, 1970, 1971; Edmunds and Thompson, 1972; Rudman, 1973a, b, 1977, 1978, 1979, 1980, 1981a, b, 1982a, b, 1984). Although about 200 species have been recorded in the literature, many more species occur there (Rudman, pers. comm.).

Lack of distributional information from areas surrounding a particular region, can lead to incorrect biogeographical conclusions, particularly in the case of erroneous assumptions of endemism.

Changes in the systematics of taxa can also alter biogeographical conclusions. For example, *Aeolidiella saldanhensis* Barnard and *A. multicolor* Macnae were thought to represent distinct endemic species in southern Africa. Recent taxonomic revisions (Gosliner and Griffiths, 1981) demonstrated that both species are junior synonyms of a widespread, circumtropical species.

Another factor which should be considered in any biogeographical study is the potential alteration of natural distributional patterns by human intervention. The prey of opisthobranch gastropods are frequently colonial organisms such as hydroids, bryozoans and sponges, which are known to foul ships' hulls. Nudibranchs, often with their food and egg masses, can be transported long distances in this manner. These introduced species have limited ranges where they become established, and are generally restricted to harbors. There is no evidence that over time, they expand their ranges appreciably.

There appears to be at least one example of the introduction of an opisthobranch species into South African waters by this means. The natural range of *Catriona columbiana* (O'Donoghue) is from the Pacific coast of North America to Japan (Baba and Hamatani, 1963). In South Africa it has been found only in Cape Town Harbor and its presence there is probably a result of international shipping (Gosliner and Griffiths, 1981).

In another instance, *Thecacera pennigera* (Montagu) is known from England, Brazil, Ghana, Japan, Australia, New Zealand and South Africa. Willan (1976) suggested that the species owes much of its distribution to transport by shipping. However, *T. pennigera* is commonly found along the coast of southern Africa from Cape Town to Umgazana. While it is found in harbors, several localities are over 250 km from the nearest harbor. Though it is possible that this species could have been distributed more widely in southern Africa following its introduction, this scenario seems unlikely. Most species that are known to be introduced retain a restricted range for extensive periods of time. Willan and Coleman (1984) have similarly suggested that *Polycera hedgpethi* Er. Marcus, which is known from central California and Mexico, Australia, New Zealand and South Africa, has been introduced into Australia by shipping. The single locality where this species has been found in South Africa is the Keurbooms River Estuary, which is a shallow inlet devoid of major shipping. *P. hedgpethi* has not been found in any large harbor in southern Africa, despite concerted collecting efforts. In the cases of *T. pennigera* and *P. hedgpethi*, it therefore does not seem reasonable to ascribe their presence in southern African waters solely to human introduction.

DIVISION OF BIOGEOGRAPHICAL PROVINCES

Most studies of the biogeography of southern Africa have focused upon the subdivision of the coastline into biogeographical provinces (Stephenson, 1948; Day, 1967; Briggs, 1974; Griffiths, 1974; Brown and Jarman, 1978; Kensley,1981). Kensley (1983) noted that these divisions are the subject of much controversy. Most of the above authors have considered the same five provincial areas: West African, cold Atlantic temperate, warm Indian temperate, subtropical east coast and tropical east coast. These areas overlap to varying degrees. Briggs (1974) distinguished two warm temperate provinces in southern Africa, bordered by tropical regions to the north.

While there are insufficient data to say much about the West African-Cold Temperate provincial boundary for opisthobranchs, data for other areas within the region suggest a great deal about provincial boundaries. Brown and Jarman (1978), noting that the Cape Peninsula separates the Atlantic Ocean from False Bay, emphasized that the temperature difference between the two sides of the peninsula may exceed 8ºC. One would, therefore, expect the Cape Peninsula to provide a significant biogeographical barrier. However, Brown and Jarman noted that 57% of the invertebrate species present in False Bay are also present along the Atlantic coast of the peninsula. This is also true for opisthobranch gastropods, where at least 69.4% of the species present in False Bay are also present along the Atlantic coast. Brown and Jarman suggested that the area from False Bay to Cape Agulhas can be considered as transitional between cold and warm temperate faunas. Of the species of opisthobranchs present at Knysna, to the east of Cape Agulhas, 59% are also found along the Atlantic coast of the Cape Peninsula. There appears to be little change in the opisthobranch fauna between the Atlantic coast of the Cape Peninsula and the warm temperate region. Rather, there appears to be a gradual dropping out and replacement of species. Millard (1978) found even less difference between the cold and warm-water temperate hydroid faunas in southern Africa than found here for opisthobranchs.

The same can be stated with regard to the boundary between the subtropical and tropical east coast provinces. There appears to be considerable similarity between the faunas present at Umgazana, Durban and Sodwana Bay. Approximately 80% of the species found at Umgazana and Durban are also found at Sodwana Bay. Clearly, Durban and Umgazana represent attenuations of the tropical fauna and have few opisthobranchs which are unique to them.

The differences in provincial overlap for opisthobranchs can best be summarized by comparison of Jaccard's Coefficient of Similarity (Valentine, 1966) between areas (Table 1). The greatest faunistic difference between adjacent areas occurs between Port Elizabeth and Umgazana. This difference corresponds to the shift between largely endemic and Atlantic species in temperate waters to Indo-Pacific and circumtropical species in the subtropics and tropics (Fig. 2).

Valentine (1966) calculated Jaccard's coefficients for adjacent faunistic provinces and subprovinces along the Pacific coast of North America. When values for southern African opisthobranchs are compared with these it is apparent that most adjacent areas appear to approach the subprovincial levels described by Valentine. The notable exception to this is the temperate/tropical boundary present between Port Elizabeth and Umgazana.

Stephenson *et al.* (1937) described the Cape Peninsula as one of the few places in the world "where water of such different temperature is separated by so little land." It

Table 1. Coefficients of faunistic similarity between areas.

	FB	KN	PE	UM	DU	SO
CT	.60	.45	.34	.09	.05	.02
FB	–	.59	.48	.14	.09	.05
KN	–	–	.54	.21	.10	.08
PE	–	–	–	.33	.19	.12
UM	–	–	–	–	.47	.26
DU	–	–	–	–	–	.63

is, therefore, remarkable that the greatest faunisitic differences do not correspond to this area of profound physical oceanographic divergence, but rather to the break between temperate and tropical species between Port Elizabeth and Umgazana. The provincial boundaries in southern Africa appear to vary between higher taxa. For this reason, it is not particularly informative to stress provincial boundaries, but rather to regard them as convenient generalizations that can be employed to subdivide the biota.

RELATIONSHIPS OF INDO-PACIFIC TAXA WITHIN TROPICAL SOUTHERN AFRICA

Recent studies of the biogeography of marine organisms in the Indian and Pacific Oceans have focused on the consideration of possible vicariant events that isolated organisms inhabiting the Pacific Plate from those inhabiting the Indo-West Pacific (Kay, 1980, 1984; Springer, 1982; Kohn, 1983). Springer, in particular, has suggested that tectonic activity between the Pacific and Indian-Australian Plates has isolated the regions from each other, resulting in subsequent speciation. Newman (1987) suggested that changes in sea level, rather than tectonic events, could have been the primary isolating mechanisms of faunas on the Pacific Plate. Springer (1982) suggested that about 20-25% of the shorefish species present on the Pacific Plate are endemic to the plate. Kay (1979) noted that approximately 20% of the Hawaiian molluscan fauna is endemic to the islands. She (1984) provided an average estimate of endemism of marine organisms on the Pacific Plate at about 40% of the total fauna, based on data for a small sample of taxa which have been well studied. Included in this figure is 52% of the fish fauna, a significantly higher level of plate endemism than suggested by Springer. Data available for Pacific Plate opisthobranchs (Er. Marcus and Burch, 1965; Kay, 1967, 1979; Kay and Young, 1969; Gosliner, 1980; Bertsch and Johnson, 1981; Johnson and Boucher, 1984) suggest that approximately 20% of the species are endemic to the plate. The extent of Pacific Plate endemism is poorly understood for most groups of marine organisms. In many cases it is not known whether endemic species are widespread on the plate or whether they are limited to a single archipelago or island. More data are required to shed light on this significant issue.

The Indo-Pacific faunal component of the southern African opisthobranch fauna exhibits a distinct distributional pattern. Eighteen percent of the species are known only from the western Indian Ocean. The other 82% of the species present in southern Africa are also known to occur at the eastern extreme of the Indian Ocean. Fifty-seven percent of the southern African Indo-Pacific opisthobranchs also are found on the non-marginal portions of the Pacific Plate. This figure attests to the fact that many of the species known to occur in southern Africa are exceedingly widespread tropical taxa.

Although 18% of the opisthobranchs species appear to be restricted to the western Indian Ocean, insufficient data are presently available to authoritatively calculate the extent of the range of some species. For example, *Chromodoris annulata* Eliot was believed to be restricted to the western Indian Ocean, from the Red Sea to South Africa (Rudman, 1973a). Recently, however, it has been recorded from the Gulf of California (Bertsch and Kerstitch, 1984).

Despite possible inaccuracies, the similarity in the extent of the range of southern African opisthobranch and prosobranch species within the Indo-Pacific, is noteworthy. Based on records of Indo-Pacific prosobranchs previously recorded from southern Africa, 23% appear to be restricted to the western Indian Ocean, 76% are found eastward to the western margin of the Pacific Plate and 59% of the total extend into the non-marginal portions of the Pacific Plate.

SISTER GROUP RELATIONSHIPS AND VICARIANCE IN SOUTHERN AFRICAN OPISTHOBRANCHS

The fact that the marine biota of southern Africa shares species with the North Atlantic, the sub-Antarctic and the Indo-Pacific is well established (Brown and Jarman, 1978; Kensley, 1981; Kilburn and Rippey, 1982). Kilburn and Rippey (1982) suggested that only 1-2% of the mollusk species within the region are also known from other southern oceanic regions. This figure is based solely on present distributional patterns of extant species and does not reflect historical events. When one examines the present distributions of the opisthobranch species of southern Africa, we find that none of the species present in the region are also found in other southern ocean localities. However, when we examine the probable sister species of the endemic opisthobranch species, a different pattern emerges. Probable sister species can be inferred with some degree of confidence for 48 of the 77 endemic species of opisthobranchs (Table 2). In several cases the inferences are easy to make (e.g. species of *Gargamella* are found only in the Sub-Antarctic and southern Africa). In other cases sister species have been determined on the basis of synapomorphies determined by methods described by Gosliner and Ghiselin (1984). Of these sister species, 25% are Indo-Pacific, 31% are known from other southern oceanic regions and 43% are known from the North Atlantic. These data suggest that, while there is currently little interchange with other southern cold-temperate and sub-Antarctic oceans, in the past southern Africa shared a significant number of species with the sub-Antarctic. Similarly, phylogenetic and biogeographical links with the Indo-Pacific have probably been present for a considerable period and have persisted to the present.

When considering vicariant events and their roles in producing various distributional patterns, most recent biogeographers have been primarily concerned with plate tectonic events as isolating mechanisms. The sister group relationships of the endemic species to sub-Antarctic species, with no extant species exhibiting this distributional pattern, suggests that this vicariant event could have occurred prior to those that isolated southern African species from conspecifics in the Indo-Pacific or North Atlantic. While these speciation events could be correlated with the breaking up of Gondwanaland, another hypothesis could better explain the Sub-Antarctic sister group relationships of these species. Newman (1979) has hypothesized that barnacle distributions in the southern oceans became established long after the

Table 2. Possible sister species of southern African endemics.

South African endemic	Sister species	Sister species range
Ringicula turtoni Bartsch	*R. australis* Hinds	Indo-Pacific
Melanochlamys sp.	*M. seurati* (Vayssière)	Mediterranean
Philinopsis capensis (Bergh)	*P. cyanea* (Martens)	Indo-Pacific
Gastropteron flavobrunneum Gosliner	*G. pohnpei* Hoff and Carlson	Indo-Pacific
G. alboaurantium Gosliner	*G. pohnpei* Hoff and Carlson	Indo-Pacific
Haminoea alfredensis Bartsch	*H. navicula* (de Costa)	N. Atlantic
Oxynoe sp.	*O. viridis* (Pease)	Indo-Pacific
Aplysiopsis sinusmensalis (Macnae)	*A. formosa* Pruvot-Fol	Mediterranean
Bursatella leachii africana (Engel)	*B. leachii leachii* (Blainville)	Indo-Pacific
Berthella sp.	*B. sideralis* (Lovén)	N. Atlantic
Pleurobranchus nigropunctatus (Bergh)	*P. albiguttatus* (Bergh)	Indo-Pacific
Pleurobranchaea bubala Ev. Marcus and Gosliner	*P. tarda* Verrill	N. Atlantic
Geitodoris capensis Bergh	*G. planata* (Alder and Hancock)	N. Atlantic
Aphelodoris brunnea Bergh	*A. varia* (Abraham)	N.S.W. Australia
A. sp.	*A. luctuosa* Bergh	New Zealand
Gargamella sp. 1	*G. latior* Odhner	S. America
G. sp. 2	*G. latior* Odhner	S. America
Rostanga sp.	*Boreodoris setidens* Odhner	N. Atlantic
Aldisa benguelae Gosliner, in Millen and Gosliner	*A. banyulensis* Pruvot-Fol	N. Atlantic
Aldisa trimaculata Gosliner, in Millen and Gosliner	*A. zetlandica* (Alder and Hancock)	N. Atlantic
Ceratosoma sp.	*C. brevicaudatum* Abraham	s. Australia
Chromodoris sp.	*C. splendida* (Angas)	s. Australia
Hypselodoris capensis (Barnard)	*H. carnea* (Bergh)	Indo-Pacific
Dendrodoris caesia (Bergh)	*D. grandiflora* (von Rapp)	N. Atlantic
Corambe sp.	*C. testudinaria* Fischer	N. Atlantic
Goniodoris mercurialis Macnae	*G. castanea* Alder and Hancock	N. Atlantic
Trapania sp.	*T. lineata* Haefelfinger	N. Atlantic
Polycera capensis Quoy and Gaimard	*P. quadrilineata* Müller	N. Atlantic
Lecithophorus capensis Macnae	*Paliolla cooki* (Angas)	s. Australia
L. sp.	*P. cooki* (Angas)	s. Australia
Tambja capensis (Bergh)	*T. morosa* (Bergh)	Indo-Pacific
Acanthodoris sp.	*A. molicella* Abraham	Auckland Is.
Melibe rosea Rang	*M. australis* (Angas)	s. Australia
Melibe liltvedi Gosliner	*M. australis* (Angas)	s. Australia
Leminda millecra Griffiths	*Telarma antarctica* Odhner	Antarctica
Dermatobranchus sp. 1	genus restricted to Indo-Pacific	
D. sp. 2	genus restricted to Indo-Pacific	
Bonisa nakaza Gosliner	*Galeojanolus ionnae* Miller	New Zealand
Janolus capensis Bergh	*J. novozealandica* (Eliot)	New Zealand
J. longidentatus Gosliner	*J. novozealandica* (Eliot)	New Zealand
Flabellina capensis (Thiele)	*F. lineata* (Alder and Hancock)	N. Atlantic
F. funeka Gosliner and Griffiths	*F. affinis* (Gmelin)	Mediterranean
F. sp.	*F. albomarginata* (Miller)	New Zealand
Cuthona speciosa (Macnae)	*C. caerulea* (Montagu)	N. Atlantic
Facelina olivacea Macnae	*F. bostoniensis* (Couthouy)	N. Atlantic
Caloria sp.	*C. elegans* (Alder and Hancock)	N. Atlantic
Amanda armata Macnae	*Nanuca sebastiani* Er. Marcus	N. Atlantic
Cratena capensis Barnard	*C. peregrina* (Gmelin)	Mediterranean

fragmentation of Gondwanaland and are largely a result of dispersal, followed by subsequent vicariance. The same could also be true of most other marine taxa in the southern hemisphere.

Tankard and Rogers (1978), Hendey (1981) and Olson (1983) have described the paleoecology of the Atlantic coast of South Africa during the Miocene and early Pliocene. Their studies of vertebrate fossils indicate that in the Miocene subtropical environments were present along the coast. During the early Pliocene, ocean temperatures began to drop markedly and the terrestrial environment became significantly drier. Fossil sea birds from the Pliocene (Olson, 1983) include many taxa that are today present in the sub-Antarctic but are absent from southern Africa. It is likely that during this period many species of marine organisms were widely distributed throughout the southern oceans. Vicariant events, such as oceanic warming during portions of the Pleistocene, could have served as isolating mechanisms that resulted in speciation within these widely distributed sub-Antarctic species.

When one examines the species that presently have disjunct distributions between southern Africa and the northern Atlantic, such as *Limacia clavigera* (Müller) and *Tritonia nilsodhneri* Ev. Marcus, and the species that have sister group relationships to the North Atlantic [e.g. *Flabellina capensis* with *F. lineata* and *F. browni* (Picton)], one finds that tectonic explanations cannot account for this vicariance. Populations of species present in southern Africa are geographically isolated and disjunct from those in the North Atlantic and are here considered to be relictual. A similar situation exists on both sides of the Isthmus of Panama, where many opisthobranch species have populations that are clearly isolated yet recognizable speciation has not occurred. The cold water environment along the Atlantic coast of southern Africa appears to be a relatively recent phenomenon. Late Pleistocene molluscan assemblages along the Atlantic coast of southern Africa suggest strong biogeographical links with West Africa and the Mediterranean (Tankard, 1975). The fact that many extant species of southern African opisthobranchs are also present in the North Atlantic indicates that little speciation has taken place and suggests that the isolation of the populations represents a relatively recent event. Several of the Atlantic species, such as *Retusa truncatula* and *Polycera quadrilineata*, are absent from the Atlantic coast of southern Africa and are restricted to warmer temperate waters of the region. This is further suggestive that these species are warm water relicts within southern Africa and implies that major climatic shifts by means of changes in oceanic currents could have a profound effect upon the evolution of marine faunas.

COMPARISON OF LEVELS OF ENDEMISM OF OPISTHOBRANCHS WITH OTHER SOUTHERN AFRICAN MARINE TAXA

Brown and Jarman (1978) demonstrated that within the southern African marine biota there are notable differences in biogeographical relationships between different taxa. For example, polychaete annelids within False Bay exhibit low levels of endemism (37.3% of the species are endemic) while echinoderms exhibit a high degree of endemism (82.4%). Similarly, Kensley (1983) has shown marked differences between the amphipod, isopod and decapod crustacean faunas. When one compares the data available for other mollusks (Kilburn and Rippey, 1982) with those for opisthobranchs, one finds that there are some significant differences (Figs. 2, 3). The non-opisthobranch mollusks exhibit a high level of endemism throughout all of southern Africa, while in the opisthobranchs there is a marked shift from endemic to Indo-Pacific species between the warm temperate and tropical regions. Even where endemism is high among opisthobranchs, it is significantly less than in non-opisthobranchs. Similarly, the percentage of Atlantic and Indo-Pacific species of non-opisthobranchs is much lower in every region than in opisthobranchs. In general, opisthobranchs within southern Africa appear to be more widespread than are other mollusks. This difference does not appear to be a taxonomic artifact, as the systematics of prosobranchs and opisthobranchs within the region are at about the same level of refinement.

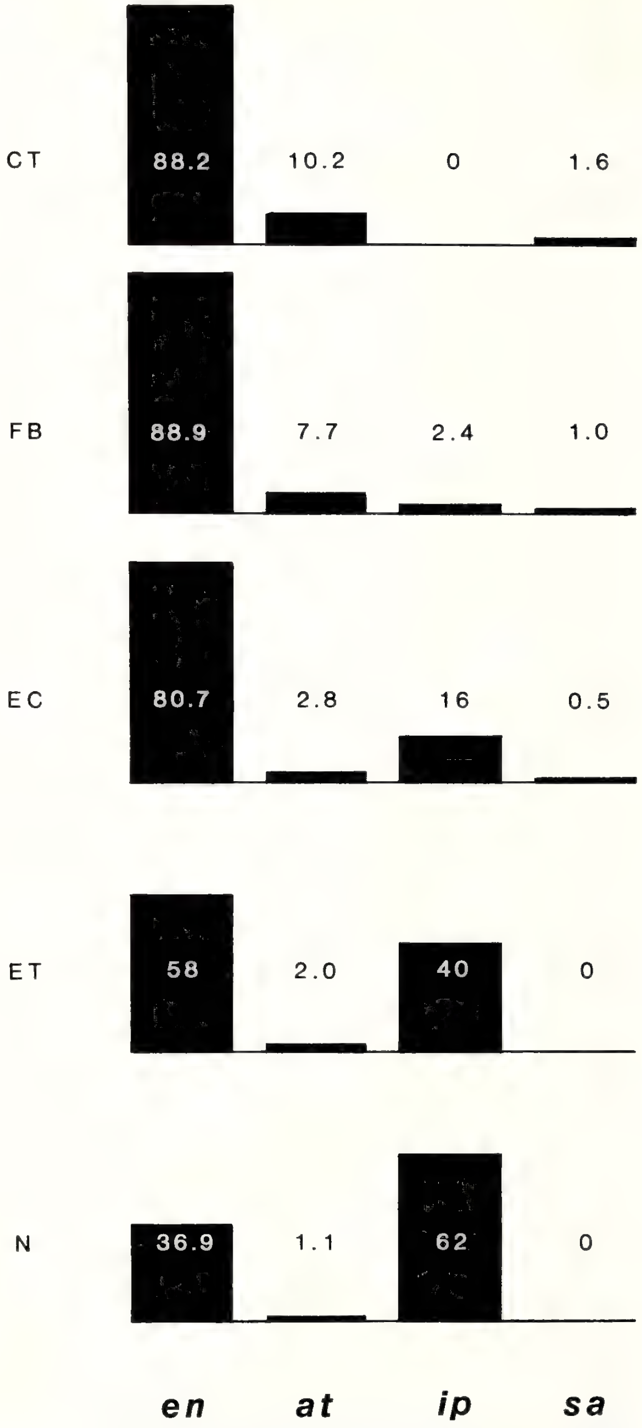

Fig. 3. Biogeographical affinities of southern African prosobranchs and bivalves (data extracted from Kilburn and Rippey, 1982) (CT - Cape Town, FB - False Bay, EC - East Cape, ET - Eastern Transkei, N - Natal, en - endemic, at - Atlantic, in - Indo-Pacific, sa - South American/South Atlantic islands).

Comparable differences in levels of endemism between molluscan taxa have been previously noted in southern Africa. Kilburn and Rippey (1982) noted that the Cypraeidae of western Transkei are largely Indo-Pacific while the Conidae of the same region are largely endemic. Similar biogeographical differences between taxa have been described from other regions of the world. Kay (1984) described less endemism among Hawaiian bivalves than among gastropods. She presented many other documented cases of divergent biogeographical affinity in a variety of organisms from throughout the Indo-Pacific.

Distinct distributional patterns between different opisthobranch taxa have been previously described. Bertsch (1972) noted that within the Panamic Province a large proportion of anaspidean opisthobranchs have circumtropical ranges while other taxa such as nudibranchs and cephalaspideans are distributed over a much narrower geographical range. Anaspideans, which are relatively well studied, appear to be more widespread in their distributions than other opisthobranch taxa.

These facts are suggestive of variable degrees of isolation of different taxa and imply that within the marine realm it is difficult to apply a single series of vicariant events to explain the biogeographical history of the entire biota.

LEVELS OF ENDEMISM AND THE TESTING OF VICARIANT HYPOTHESES

Nelson and Platnick (1981) have discounted the significance of disparity in levels of endemism (proportion of species of a particular taxon that are endemic to a region) between higher taxa and their role in explaining differences in vicariant history. They suggested that most differences in levels of endemism are merely taxonomic artifacts of lumping versus splitting. They further suggested (p. 489), that with greater taxonomic precision, "one might expect that most native Hawaiian marine organisms might ultimately be regarded as endemic, as is the case for land plants." Kay (1980) stated that there are qualitative differences between the levels of endemism of marine and terrestrial biota of the Hawaiian Islands and more recently (1984) contradicted Nelson and Platnick's assertion, noting that Hawaiian marine endemics have undergone little or no adaptive radiation.

Scheltema (1971a), Scheltema and Williams (1983) and Kay (1980, 1984) have noted differences in dispersal capabilities of marine organisms and have correlated these with biogeographical distributions. As one could predict, species with direct development are far less widely distributed than species with planktotrophic larvae. Kempf (1981) demonstrated that at least one species of opisthobranch can maintain viable larvae in the plankton in excess of 200 days. Springer (1982) suggested that in Indo-Pacific reef fishes, species with non-planktonic development can be as widely distributed as those with planktonic larvae. The correlation between life history adaptations and distribution requires more study.

Data available for southern African marine mollusks shed some light on the issue. There are differences in the levels of endemism between prosobranch and opisthobranch gastropods (Figs. 2, 3) within the region and these differences occur at all seven localities surveyed within southern Africa. If one examines the life history modes of prosobranchs and opisthobranchs there are also notable differences. Southern African prosobranch gastropods exhibit a higher incidence of direct development and species with a short larval life than do opisthobranchs. Most prosobranch taxa possess representatives with direct, lecithotrophic and planktotrophic development (e.g. Littorinidae, Neritidae, Fissurellidae, Vermetidae, Crepidulidae). In other families, such as the Buccinidae, Marginellidae and Volutidae, direct development is the dominant mode of development. Even in prosobranch taxa where planktotrophic development is generally the rule, many southern African representatives possess direct development. This is the case in the Cypraeidae (Gosliner and Liltved, 1985) and the Conidae (Kilburn and Rippey, 1982). In contrast, of the two hundred opisthobranch species studied in southern Africa, only one is known to possess direct development (Gosliner and Griffiths, 1981). Thus, there is a strong correlation between length of larval life and levels of endemism in southern African marine mollusks.

Similarly, Kensley (1983) has shown that decapod crustaceans exhibit less endemism in southern Africa than do amphipods and isopods. Most decapods have pelagic larval stages while most amphipods and isopods brood their young. The polychaete annelids in southern Africa have a low degree of endemism. The overwhelming number of species have pelagic larvae and are widely distributed.

Nelson and Platnick (1981) stated that levels of endemism are irrelevant with regard to the cladistic aspect of biogeography. This does not appear to be the case in the southern African marine biota. As noted above, the endemic Cypraeidae of southern Africa, in species where it has been studied, all have direct development (Gosliner and Liltved, 1985). This appears to be a synapomorphy, which together with morphological data, unites the southern African taxa with their sister group in southern Australia. In this case, at least, life history strategies, sister group relationships and levels of endemism are all strongly linked. Levels of endemism are significant in biogeographical studies and differences in endemism could have strong biological and cladistic bases.

Life history modes may not be the only biological bases for producing differences in levels of endemism. Stanley (1979) suggested that there could be a correlation between patterns of extinction and degree of endemism. He has also examined variable rates of speciation between bivalves and gastropods. Kay (1984) has discussed some of these other possible reasons for discordance in biogeographical data.

Vicariance biogeographers (Nelson and Platnick, 1981) claim to construct and test hypotheses of biogeographical relationships. To discount major differences in levels of endemism between taxa as mere artifacts of taxonomy is subjective judgement without factual support. One cannot simply discard data that challenge an hypothesis. As Kay (1980) pointed out, the fact that 94% of the vascular flora and 80-90% of the terrestrial mollusks are endemic to Hawaii while only 20% of the marine mollusks are endemic, suggests that evolution of marine and terrestrial organisms has been influenced by different degrees of isolation. This fact also suggests that different vicariant events could have been important in the marine environment than in terrestrial ecosystems. If vicariance biogeographers wish to have their hypotheses taken seriously, they will have to regard such discrepancies of data as serious challenges to simplistic hypotheses rather than artifacts of human perception of systematics.

Vicariance biogeographers suggest that the only considerations to be utilized in biogeographical analysis are the determination of sister species of endemic species and their distributional patterns. There are several flaws with employing this approach to the exclusion of other pertinent data. Species that have disjunct distributions but have not yet speciated also supply information that has a direct bearing on vicariant events and biogeographical history. Consideration of only endemic species becomes potentially problematic in regions with low levels of endemism, where the likelihood that a small number of endemics and their sister species may not adequately reflect the recent vicariant events that have occurred. It appears that a more ecclectic approach, integrating vicariance biogeography and present distributional patterns, with a serious attempt to incorporate biological factors that could alter those patterns, will produce a far more coherent picture of the biogeography of organisms.

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Appendix 1. Distributions of southern African Opisthobranchs. Listed below are the taxa that have sufficiently reliable distributional data to infer biogeographical relationships. For each species its distribution outside of southern Africa is presented as A-Atlantic, CO-Cosmopolitan, CT-Circumtropical, E-Endemic or IP-Indo-Pacific. Its range is then presented. For species with Indo-Pacific distributions the known eastern limit of its distribution is presented in parentheses. Immediately following the distribution outside of southern Africa is an indication of the distribution of each species within southern Africa. The following numerals indicate geographical regions within southern Africa and correspond to those of Figure 1: 1-Cape Town; 2-False Bay; 3-Knysna; 4-Port Elizabeth; 5-Umgazana; 6-Durban; 7-Sodwana Bay. A species with a range of 3-7 is known from the Knysna region to the Sodwana Bay area.

Class Gastropoda
Subclass Opisthobranchia

Order Cephalaspidea
Family Ringiculidae
- *Ringicula turtoni* Bartsch, 1915, E, 4-7.

Family Acteonidae
- *Acteon flammeus* (Gmelin, 1791), IP (Fiji), 6-7.
- *A. fortis* Thiele, 1925, IP (East Africa), 6-7.
- *Pupa affinis* (A. Adams, 1854), IP (Arabian Sea), 6-7.
- *P. solidula* (Linnaeus, 1758), IP (Tahiti), 6-7.
- *P. sulcata* (Gmelin, 1791), IP (Fanning Island), 6-7.
- *P. suturalis* (A. Adams, 1854), IP (Madagascar), 6-7.
- *P. tessellata* (Reeve, 1842), IP (Hawaii), 6-7.
- *Rictaxis albus* (Sowerby, 1873), E, 2-7.

Family Bullinidae
- *Bullina lineata* (Gray, 1825), IP (Hawaii), 5-7.

Family Hydatinidae
- *Hydatina albocincta* (van der Hoeven, 1811), IP (Hawaii), 6-7.
- *H. amplustre* (Linnaeus, 1758), IP (Hawaii, Tahiti), 6-7.
- *H. physis* (Linnaeus, 1758), CT (Caribbean, IP to Hawaii), 6-7.
- *H. zonata* (Lightfoot, 1786), IP (Japan), 6-7.
- *Micromelo undata* (Brugière, 1792), CT (Caribbean, IP to Hawaii), 6-7.

Family Retusidae
- *Retusa truncatula* (Brugière, 1792), A (European Atlantic, Canary Is), 2-6.

Family Scaphandridae
- *Acteocina smithi* (Bartsch, 1915), E, 4-7.
- *Cylichna tubulosa* Gould, 1859, E, 1-6.
- *Scaphander punctostriatus* (Mighels, 1841), A (W. and E. Atlantic), 1.

Family Aglajidae
- *Chelidonura fulvipunctata* Baba, 1938, CT (Mediterranean, IP to Japan), 3-7.
- *C. hirundinina* (Quoy and Gaimard, 1824), CT (Caribbean, IP to Hawaii), 5-7.
- *Melanochlamys* sp., E, 2.
- *Philinopsis capensis* (Bergh, 1907), E, 2-4.
- *P. cyanea* (Martens, 1879), IP (Australia), 6-7.

Family Gastropteridae
- *Gastropteron alboaurantium* Gosliner, 1984, E, 1.
- *G. flavobrunneum* Gosliner, 1984, E, 1.

Family Haminoeidae
- *Atys cylindrica* (Helbling, 1779), IP (Fanning Island), 6-7.
- *Haminoea alfredensis* Bartsch, 1915, E, 1-4.
- *H. natalensis* (Krauss, 1848), IP (Seychelles), 5-7.

Phaneropthalmus smaragdinus (Rüppell and Leuckart, 1831), IP (Easter Is.), 7.
Smaragdinella calyculata (Broderip and Sowerby, 1829), IP (Easter Is.), 7.
Family Bullidae
Bulla ampulla (Linnaeus, 1758), IP (Central Pacific), 4-7.

Order Sacoglossa
Family Cylindrobullidae
Ascobulla fischeri (Adams and Angas, 1864), IP (Australia), 2-7.
Volvatella laguncula Sowerby, 1894, E, 2-4.
Family Juliidae
Berthelinia schlumbergeri Dautzenberg, 1895, IP (Hawaii), 7.
Julia zebra Kawaguti, 1981, IP (Easter Is.), 7.
Family Oxynoidae
Lobiger souverbiei Fischer, 1856, CT (Caribbean, Mediterranean, IP to Pacific North America), 7.
Lophopleurella capensis (Thiele, 1912), E, 2.
Oxynoe viridis (Pease, 1861), IP (Pacific North America), 6-7.
O. sp., E, 2-3.
Family Elysiidae
Elysia halimedae Macnae, 1954, IP (Hawaii), 5-7.
E. livida Baba, 1955, IP (Enewetak), 7.
E. marginata (Pease, 1871), IP (Fanning Is.), 6-7.
E. moebii (Bergh, 1888), IP (Mauritius), 7.
E. rufescens (Pease, 1871), IP (Tahiti), 7.
E. vatae Risbec, 1928, IP (Enewetak), 7.
E. virgata (Bergh, 1888), IP (Mauritius), 7.
E. viridis (Montagu, 1804), A (European Atlantic, Mediterranean), 1-6.
Family Stiligeridae
Placida dendritica (Alder and Hancock, 1843), CO (W. and European Atlantic, Mediterranean, Japan, Australia, California), 1-4.
Stiliger ornatus Ehrenberg, 1831, IP (Japan), 7.
Family Caliphyliidae
Aplysiopsis sinusmensalis (Macnae, 1954), E, 1-2.
Phyllobranchillus orientalis (Kelaart, 1858), IP (Hawaii), 6-7.

Order Anaspidea
Family Akeridae
Akera soluta (Gmelin, 1791), IP (Enewetak), 3-7.
Family Aplysiidae
Aplysia dactylomela Rang, 1828, CT (Caribbean, Ghana, IP to Pacific North America), 4-7.
A. juliana Quoy and Gaimard, 1832, CT (Caribbean, Ghana, IP to Pacific North America). 1-7.
A. oculifera Adams and Reeve, 1850, IP (Hawaii), 2-7.
A. parvula Mörch, 1863, CT (W. and E. Atlantic, IP to Pacific North America), 1-7.
Dolabella auricularia (Solander, 1786), IP (Pacific North America), 3-7.
Family Notarchidae
Bursatella leachii leachii (Blainville, 1817), IP (New Zealand), 6-7.
B. leachii africana (Engel, 1927), E, 2-4.
Dolabrifera dolabrifera (Rang, 1828), CT (Caribbean, Ghana, IP to Pacific North America), 6-7.
Stylocheilus longicauda (Quoy and Gaimard, 1824), CT (Caribbean, IP to Pacific North America), 5-7.

Order Notaspidea
Family Umbraculidae
Tylodina alfredensis Turton, 1932, E, 4.
Umbraculum sinicum (Gmelin, 1783), CT (Caribbean, Mediterranean, IP to Pacific North America), 5-7.
Family Pleurobranchidae
Berthella plumula (Montagu, 1803), A (European Atlantic, Mediterranean), 1-3.
B. tupala Marcus, 1957, CT (Caribbean, IP to Hawaii) 5.
B. sp. E, 1.
Berthellina citrina (Rüppell and Leuckart, 1828), IP (Hawaii), 1-7.
Pleurobranchus inhacae Macnae, 1962, IP (Mauritius), 6-7.
P. peronii Cuvier, 1805, IP (Hawaii), 6-7.
P. xhosa Macnae, 1962, IP (Seychelles), 5-7.
P. nigropunctatus (Bergh, 1907), E, 2-4.
Family Pleurobranchaeidae
Euselonops luniceps (Cuvier, 1817), IP (Hawaii), 7.
P. brockii Bergh, 1897, IP (East Africa), 7.
P. bubala Ev. Marcus and Gosliner, 1984, E, 1-3.
P. tarda Verrill, 1880, A (Atlantic North America, W. Africa), 1-3.
Pleurobranchella nicobarica Thiele, 1925, IP (Nicobares Is.), 7.

Order Nudibranchia
Suborder Doridacea
Family Bathydorididae
Doriodoxa benthalis Barnard, 1963, E, 1.
Family Dorididae
Atagema gibba Pruvot-Fol, 1951, A (European Atlantic, Mediterranean), 3.
A. rugosa Pruvot-Fol, 1951, A (Mediterranean), 1.
Doriopsis pecten (Collingwood, 1881), IP (Hawaii), 6-7.
Doris verrucosa Linnaeus, 1758, A (W. and E. Atlantic), 1-3.
D. sp., IP (Tanzania), 7.
Family Discodorididae
Discodoris fragilis (Alder and Hancock, 1864), CT (Canary Is., IP to Hawaii), 5-7.
D. sp., E, 1-2.
Geitodoris capensis Bergh, 1907, E, 1-4.
Family Asteronotidae
Aphelodoris brunnea Bergh, 1907, E, 2-4.
A. sp., E, 1-3.
Artachaea sp., E, 3.
Halgerda formosa Bergh, 1880, IP (Mauritius), 6-7.
H. punctata Farran, 1905, IP (Sri Lanka), 7.
H. wasinensis Eliot, 1904, IP (Enewetak), 7.
Sclerodoris apiculata (Alder and Hancock, 1864), IP (India), 5-7.
S. coriacea Eliot, 1904, (Tanzania), 7.
Family Kentrodorididae
Gargamella sp. 1, E, 2.
G. sp. 2, E, 2.
Jorunna tomentosa (Cuvier, 1804), A (European Atlantic), 1-3.
J. zania Marcus 1976, IP (Tanzania), 6-7.
Family Rostangidae
Rostanga muscula (Abraham, 1877), IP (New Zealand), 6-7.
R. sp. 1, E, 1-2.
R. sp. 2, E, 1.
Family Aldisidae
Aldisa benguelae Gosliner, in Millen and Gosliner, 1985, E, 1.
A. trimaculata Gosliner, in Millen and Gosliner, 1985, E, 1-2.
Family Platydorididae

  - *Platydoris cruenta* (Quoy and Gaimard, 1832), IP (Enewetak), 6.7.
  - *P. scabra* (Cuvier, 1806), IP (Marshall Is.), 7.
- Family Chromodorididae
  - *Cadlina* sp. 1, E, 2.
  - *C.* sp. 2, E, 1.
  - *Ceratosoma cornigerum* A. Adams and Reeve, 1850, IP (Hawaii), 7.
  - *C.* sp., E, 3.
  - *Chromodoris africana* Eliot, 1904, (Red Sea, Seychelles), 7.
  - *C. alderi* Collingwood, 1881, IP (Formosa), 6-7.
  - *C. annulata* Eliot, 1904, IP (Gulf of California), 6-7.
  - *C. aspersa* (Gould, 1852), IP (Hawaii), 6-7.
  - *C. geometrica* (Risbec, 1928), IP (Enewetak), 7.
  - *C. hamiltoni* Rudman, 1977, IP (Tanzania), 6-7.
  - *C. inopinata* Bergh, 1905, IP (Fiji), 7.
  - *C. marginata* (Pease, 1860), IP (Hawaii), 6-7.
  - *C. vicina* Eliot, 1904, IP (Tanzania), 7.
  - *C.* sp. 1, E, 1-4.
  - *C.* sp. 2, E, 1.
  - *C.* sp. 3, IP (Tanzania), 7.
  - *C.* sp. 4, IP (Seychelles), 7.
  - *C.* sp. 5, IP (Seychelles), 7.
  - *Durvilledoris leminiscata* (Quoy and Gaimard, 1832), IP (Tahiti), 6-7.
  - *Glossodoris atromarginata* (Cuvier, 1804), IP (Tahiti), 7.
  - *G.* sp., IP (Tanzania), 7.
  - *Hypselodoris carnea* (Bergh, 1889), IP (Mauritius), 5-7.
  - *H. capensis* (Barnard, 1927), E, 1-5.
  - *H. infucata* (Rüppell and Leuckart, 1828), IP (Hawaii), 6-7.
  - *H. maridadilus* Rudman, 1977, IP (Hawaii), 6-7.
  - *Noumea decussata* Risbec, 1928 (Hawaii), 5-7.
  - *N. purpurea* Baba, 1949, IP (Japan), 7.
  - *N. varians* (Pease, 1871), IP (Hawaii), 7.
  - *Risbecia pulchella* (Rüppell and Leuckart, 1828), IP (Red Sea), 6-7.
- Family Hexabranchidae
  - *Hexabranchus sanguineus* (Rüppell and Leuckart, 1828), IP (Hawaii), 5-7.
- Family Dendrodorididae
  - *Dendrodoris caesia* (Bergh, 1907), E, 1-4.
  - *D. denisoni* (Angas, 1864), IP (Hawaii), 6-7.
  - *D. nigra* (Stimpson, 1855), IP (Hawaii), 5-7.
  - *Doriopsilla miniata* (Alder and Hancock, 1864), CT (Mediterranean, IP to Australia), 1-7.
  - *D.* sp. 1, E, 1.
  - *D.* sp. 2, E, 1-3.
- Family Phyllidiidae
  - *Ceratophyllidia africana* Eliot, 1903, IP (Tanzania), 7.
  - *Phyllidia varicosa* Lamarck, 1801, IP (Hawaii), 6-7.
  - *P.* sp. 1, IP (Seychelles), 7.
  - *P.* sp. 2, IP (Seychelles), 7.
- Family Vayssieridae
  - *Okadaia elegans* Baba, 1930, IP (Hawaii), 5-7.
- Family Corambidae
  - *Corambe* sp., E, 2.
- Family Goniodoridae
  - *Ancula* sp., E, 1-2.
  - *Goniodoris castanea* Alder and Hancock, 1854, CO (European Atlantic, Mediterranean, Japan), 1-4.
  - *G. mercurialis* Macnae, 1958, E, 1-2.
  - *G. ovata* Barnard, 1934, E, 2.
  - *Okenia mediterranea* (Ihering, 1886), A (Mediterranean), 1-2.
  - *Trapania* sp., E, 3.
- Family Polyceridae
  - *Aegires* sp., E, 1-4.
  - *Crimora* sp., E, 4.
  - *Kalinga ornata* Alder and Hancock, 1864, IP (Australia), 6-7.
  - *Kaloplocamus ramosus* (Cantraine, 1835), CT (Mediterranean, IP to Australia), 2-7.
  - *Limacia clavigera* (Müller, 1776), A (European Atlantic, Mediterranean), 1-4.
  - *Plocamopherus maculatus* (Pease, 1860), IP (Hawaii), 7.
  - *Polycera capensis* Quoy and Gaimard, 1824, E (introduced in Australia), 1-4.
  - *P. hedgpethi* Er. Marcus, 1964, IP (Australia, New Zealand, Pacific North America), 3.
  - *P. quadrilineata* (Müller, 1776), A (E. Atlantic, Mediterranean), 3-4.
  - *Thecacera pacifica* (Bergh, 1884), IP (Arafura Sea), 3-7.
  - *T. pennigera* (Montagu, 1804), CO (W. and E. Atlantic, Mediterranean, Ghana, Pakistan, Australia, New Zealand, Japan), 1-5.
  - *Nembrotha lineolata* Bergh, 1905, (Japan), 6-7.
  - *N. livingstonei* Allan, 1933, IP (Australia), 6-7.
  - *Roboastra gracilis* (Bergh, 1877), IP (Australia), 7.
  - *R. luteolineata* (Baba, 1936), IP (Japan), 7.
  - *Tambja capensis* (Bergh, 1907), E, 1-4.
  - *T. morosa* (Bergh, 1877), IP (Hawaii), 7.
- Family Gymnodorididae
  - *Gymondoris alba* (Bergh, 1877), IP (Hawaii), 6-7.
  - *G. bicolor* (Alder and Hancock, 1864), IP (Hawaii), 7.
  - *G. ceylonica* (Kelaart, 1858), IP (Tahiti), 7.
  - *G. inornata* (Bergh, 1880), IP (Japan), 6-7.
  - *G. okinawae* Baba, 1936, IP (Hawaii), 7.
  - *Lecithophorus capensis* Macnae, 1958, E, 1-4.
- Family Onchidorididae
  - *Acanthodoris* sp., E, 2.
- Family Bornellidae
  - *Bornella stellifer* (Adams and Reeve in A. Adams, 1848) IP (Hawaii), 5-7.
  - *B. anguilla* Johnson, 1983, IP (Enewetak), 7.
- Family Scyllaeidae
  - *Notobryon wardi* Odhner, 1936, IP (Australia), 1-3.
- Family Tethyidae
  - *Melibe pilosa* Pease, 1860, IP (Hawaii), 7.
  - *M. rosea* Rang, 1829, E, 1-3.
  - *M. liltvedi* Gosliner, 1987, E, 1.
- Family Dotoidae
  - *Doto coronata* (Gmelin, 1791), A (E. Atlantic, Mediterranean), 1-3.
  - *D. pinnatifida* (Montagu, 1804), A (E. Atlantic, Mediterranean), 1-2.
  - *D. rosea* Trinchese, 1881, A (Mediterranean), 2.
- Family Marianinidae
  - *Marianina rosea* Pruvot-Fol, 1930, IP (Enewetak), 7.
- Family Tritoniidae
  - *Marioniopsis cyanobranchiata* (Rüppell and Leuckart, 1831), IP (Japan), 5-7.
  - *Tritonia nilsodhneri* Ev. Marcus, 1983, A (European Atlantic), 1.
  - *T.* sp. 1, E, 2-4.
  - *T.* sp. 2, E, 1-3.
- Family Lemindidae
  - *Leminda millecra* Griffiths, 1985, E, 1-6.
- Family Arminidae
  - *Armina gilchristi* (Bergh, 1907), E, 1-4.
  - *Dermatobranchus* sp. 1, E, 1-4.
  - *D.* sp. 2, E, 1.

Family Janolidae
- *Bonisa nakaza* Gosliner, 1981, E, 1-4.
- *Janolus capensis* Bergh, 1907, E, 1-4.
- *J. longidentatus* Gosliner, 1981, E, 1-2.

Family Flabellinidae
- *Flabellina capensis* (Thiele, 1925), E, 1-4.
- *F. funeka* Gosliner and Griffiths, 1981, E, 2-4.
- *F.* sp. 1, E, 2.
- *F.* sp. 2, E, 2.
- *F.* sp. 3, IP (Enewetak), 7.

Family Embletoniidae
- *Embletonia gracilis* Risbec, 1928, IP (Hawaii), 2.

Family Eubranchidae
- *Eubranchus* sp. 1, E, 1-2.
- *E.* sp. 2, E, 2-3.
- *E.* sp. 3, E, 3.

Family Tergipedidae
- *Catriona casha* Gosliner and Griffiths, 1981, E, 1-3.
- *Cuthona annulata* (Baba, 1949), IP (Japan), 7.
- *C. kanga* (Edmunds, 1970), IP (Tanzania), 7.
- *C. ornata* Baba, 1937, IP (Japan), 6-7.
- *C. speciosa* (Macnae, 1954), E, 1-4.
- *C.* sp. 1, E, 1-2.
- *C.* sp. 2, E, 1-2.
- *Phestilla melanobrachia* Bergh, 1874, IP (Hawaii), 7.
- *Tergipes tergipes* Forskäl, 1779, A (W. and E. Atlantic, Mediterranean), 1-2.

Family Fionidae
- *Fiona pinnata* (Eschscholtz, 1831), CO (all warm temperate and tropical seas), 3.

Family Facelinidae
- *Amanda armata* Macnae, 1954, E, 1-2.
- *Caloria indica* (Bergh, 1896), IP (Hawaii), 7.
- *C.* sp. 1, E, 1-2.
- *C.* sp. 2, E, 1.
- *Facelina olivacea* Macnae, 1954, E, 1-4.
- *Favorinus ghanensis* Edmunds, 1968, A (Ghana), 3.
- *F. japonicus* Baba, 1949, IP (Hawaii), 7.
- *Godiva quadricolor* (Barnard, 1927), A (Ghana), 1-4.
- *Moridilla brockii* Bergh, 1888, IP (Sundu Sea), 7.
- *Phyllodesmium hyalinum* Ehrenberg, 1831, IP (Okinawa), 7.
- *P. poindimiei* (Risbec, 1928), IP (New Caledonia), 6-7.
- *P. serratum* (Baba, 1949), IP (Japan), 2-7.
- *Pruvotfolia pselliotes* (Labbé, 1923), A (Mediterranean, Ghana), 1-4.

Family Cratenidae
- *Cratena capensis* Barnard, 1927, E, 1-4.
- *C. simba* Edmunds, 1970, 7.
- *C.* sp., E, 3.

Family Glaucidae
- *Glaucus atlanticus* Forster, 1777, CT (all tropical and warm temperate oceans), 1-7.

Family Aeolidiidae
- *Aeolidiella alba* Risbec, 1928, CT (Caribbean, IP to Pacific North America), 6-7.
- *A. indica* Bergh, 1888, CT (Caribbean, Mediterranean, IP to Pacific North America), 1-7.
- *Baeolidida palythoae* Gosliner, 1985, IP (Seychelles), 5-7.

POPULATION ECOLOGY OF CARIBBEAN ASCOGLOSSA (MOLLUSCA: OPISTHOBRANCHIA): A STUDY OF SPECIALIZED ALGAL HERBIVORES

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ABSTRACT

Ascoglossan (= Sacoglossan) populations were sampled in fifteen habitats in Florida, Belize, and Bermuda. Thirty-seven species were collected, with a maximum of thirteen species in a single habitat. Ascoglossan communities of these habitats were compared via Czekanowski's similarity coefficient. Several broad habitat types were described based on dominant vegetation, sediments, and water quality: epimanglic, epilithic, subtropical lagoon, coral-sand, and coral reef. Ascoglossan associations for most of these habitats were distinctly separable, with similarity coefficients ranging from about 75% to 20%.

Lower population densitites (biomass and number of individuals g^{-1} dry algae) occurred on coral reefs than in mangrove areas. Population density increased with latitude. Population density also decreased as dietary ash level increased.

Ascoglossan populations have potential as indicators of environmental quality, feeding on algae that occur primarily in clear water of low to moderate nutrient availability and low sediment load. Life histories and morphology of prey algae could represent adaptations to varied nutrient regimes; these life history patterns entrain those of their ascoglossan predators. Species that have high density populations and irruptive life histories generally feed on septate, seasonal algae, while low-density, stable species feed on perennial siphonaceous algae. Highly calcified algae appear resistant to ascoglossan feeding; low feeding rates could have been a strong force favoring evolution of kleptoplasty (= symbiotic chloroplasts).

The Ascoglossa are unusual animals, possessing several unique specializations. They are perhaps the most stenotrophic of marine herbivores, feeding suctorially on a wide range of marine plants (Clark and Busacca, 1978). They have highly adaptive reproduction, with a notably high incidence of encapsulated metamorphosis and lecithotrophy (Clark and Goetzfried, 1978; Clark and Jensen, 1981). Also, they are the only animals known to support "symbiotic chloroplasts" (kleptoplastids), which provide direct solar carbon fixation (Trench, 1975). Unfortunately, we know relatively little about their ecology, perhaps due to major problems in quantitative sampling (discussed below). As a result, the functions of these animals in marine ecosystems are poorly understood.

Although trophically specialized, ascoglossans as a group are broadly distributed in latitude and habitat, and exhibit a variety of life history patterns. This combination of dietary specialization with otherwise broad adaptation is uncommon among marine animals, and suggests that detailed study of life histories of ascoglossans could provide information of general interest in marine ecological theory. A paucity of data on ascoglossan populations, however, limits interpretation of their ecological significance and adaptations.

Ascoglossans are, together with herbivorous fish, the major predators of the siphonalean algae, which are the dominant primary producers in coral reef ecosystems [up to 80% of total reef calcium carbonate is produced by the genus *Halimeda* (Goreau and Goreau, 1973; Hillis-Colinvaux, 1986)]. Although the population densities of ascoglossans in the reef environment appear low, their role in reef ecology is potentially significant. An analysis of ascoglossan populations in tropical systems could greatly clarify their ecological importance.

In this study, we present quantitative population estimates from Florida and Belize, C.A., and compare these with population data from other regions. In evaluating these data, we also include descriptions of representative ascoglossan habitats and communities of the subtropical and

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tropical Caribbean province.

MATERIALS AND METHODS

Quantitative samples were collected from mangrove cays and the barrier reef near Carrie Bow Cay, Belize, C.A. and from several locations in Florida (Figs. 1, 2). Quantitative sampling generally involved a period of qualitative presampling of potential habitats and algal foods (concentrating on Siphonales, Siphonocladales, and Cladophorales), using snorkel or SCUBA. In this phase we attempted to identify "optimal" habitats as evidenced by high-density populations and the presence of mature animals. During this phase, potential algal foods were detached from the substrata and vigorously shaken underwater. The approximate numbers and species of slugs detached were noted. Evidence of feeding (evacuated algal cells and thalli) and presence of ascoglossan egg masses were typically used to locate potential study populations, but we attempted to analyze all macrophytic algae belonging to the above groups in each of the habitats. To ensure comprehensive surveys of community composition, we spent a minimum of 30 hr presampling in each study area, with total field observation time in Belize of about 300 hr and about 150 hr in Bermuda, each made during two visits. Florida observations represent cumulative studies since 1968 at various sites, with most sites studied on a monthly basis for several years.

Communities were compared on the basis of co-occurrence of species using Czekanowski's similarity coefficient (Clifford and Stephenson, 1975).

Populations from the selected microhabitats were quantified by collecting all slugs detached by the above method, using individual suction collectors (Clark, 1971) for each sample. In the case of growths of filamentous algae (e.g. *Cladophora*) we detached masses of algae containing slugs and separated slugs and eggs in the laboratory. Water temperature was measured with a stem thermometer *in situ*. After each handful of algae was processed, it was stored in a mesh collecting bag. On return to the laboratory, each algal sample was again examined for slugs possibly missed during the underwater sampling. Slugs were sorted by species, egg masses were removed if present, and slugs and eggs were counted, placed in pre-weighed foil cups, and dried. Algal samples were placed in aluminum foil pans and dried. Belizean samples were partially dried in air or a warm gas oven to prevent decomposition. All samples were dried at 80°C to constant weight before final weighing, following return to our laboratory. Portions of "anchored" siphonales (*Penicillus, Caulerpa* spp., *Udotea*) that are not used as food by ascoglossans were removed to equalize comparisons with other algae (e.g. Cladophorales) in which the entire thallus is utilized as food (Fig. 3). In general, portions with exceptionally tough cell walls [*Caulerpa paspaloides* (Bory) Greville basal stolon and lower stalk] or heavily calcified (white/yellow) portions were removed. In the less differentiated *Caulerpa* species [*C. racemosa* (Forsskål) J. Agardh, *C. verticillata* J. Agardh] the entire thallus' contents appear usable as food, and we used the entire plant in weight determinations. In many locations, slugs can be qualitatively collected but densities are below levels at which algae can be reasonably processed with our present technique (less than one animal per 100 g algal dry weight).

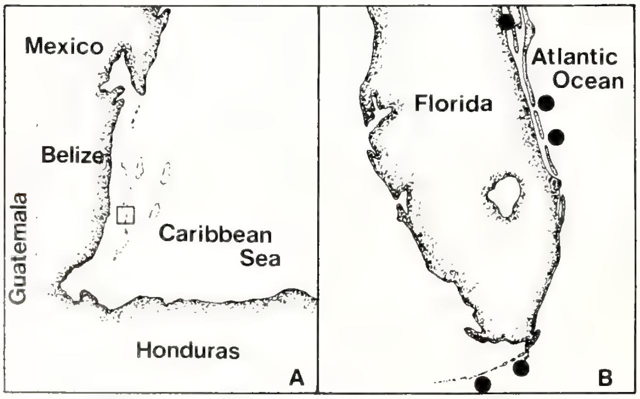


Fig. 1. Locations of principal collection sites in this study. **A.** Belizean barrier reef system. **B.** Eastern Florida, from north to south: north Indian River; Sebastian Inlet; Fort Pierce Inlet; Key Largo; Long Key.

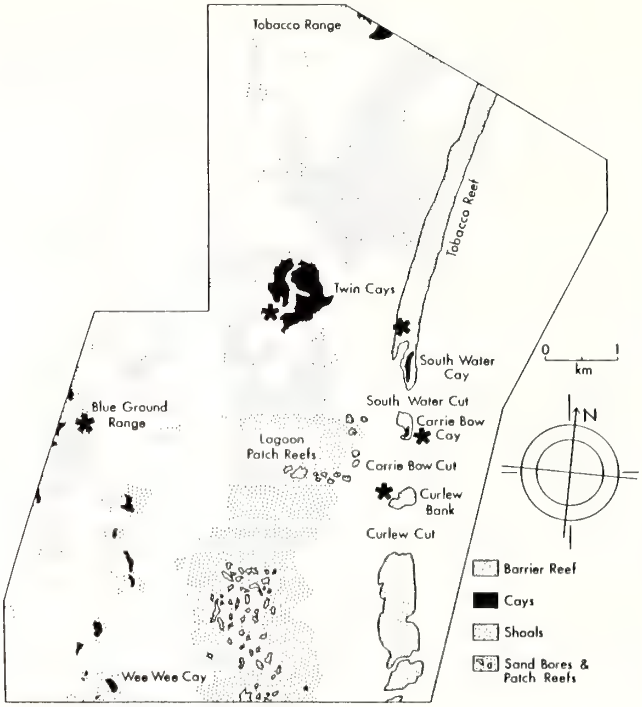


Fig. 2. Vicinity of Carrie Bow Cay, Belize and Twin Cays (from Rützler and Macintyre, 1982).

To facilitate comparison of quantitative data based on algal displacement volume or net weight, we have converted other investigators' data to approximate equivalent dry weights using Floridan congeneric algae, rinsed briefly in fresh water and oven dried at 80°C to constant weight. Data for *Limapontia capitata* (Mueller) (Jensen, 1975) were converted from displacement volume to dry weight using

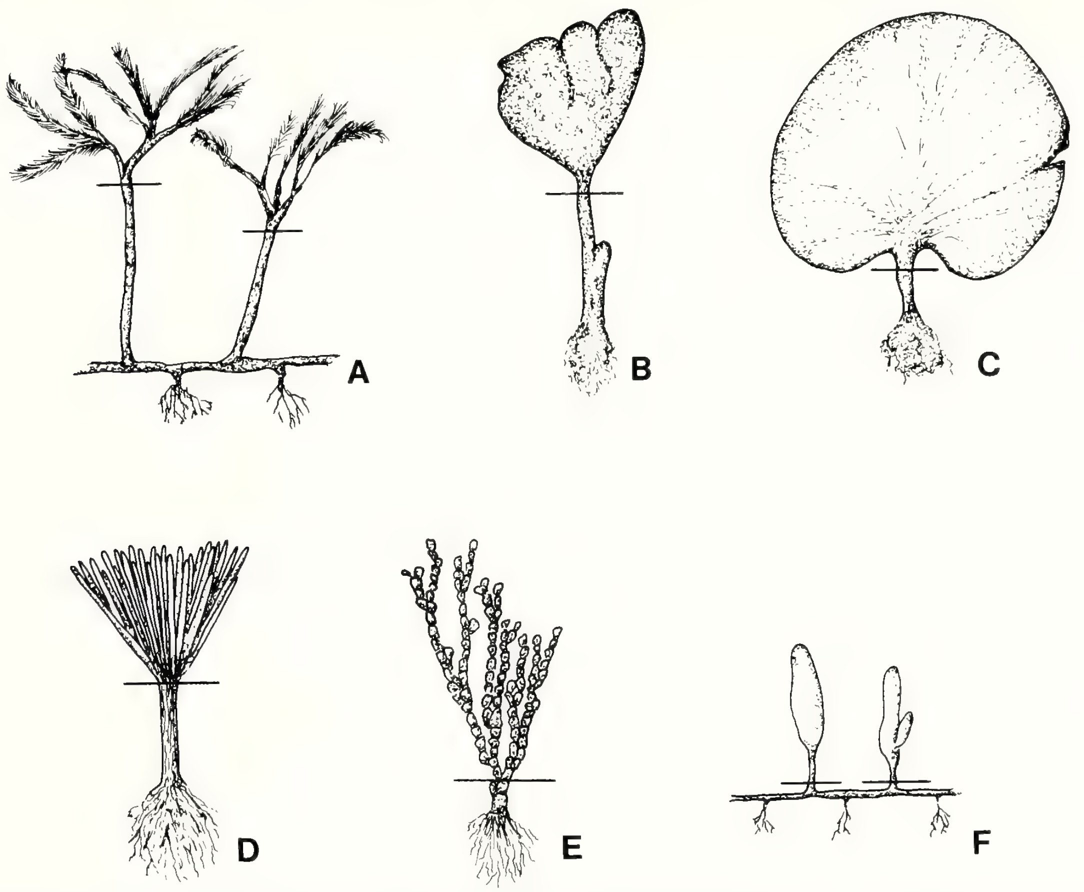


Fig. 3. Selection of tissues (distal to line) used in algal biomass and ash measurements. **A.** *Caulerpa paspaloides.* **B.** *Avrainvillea nigricans.* **C.** *Udotea conglutinata.* **D.** *Penicullus dumetosus.* **E.** *Halimeda incrassata.* **F.** *Caulerpa prolifera.*

Cladophora gracilis (Griffiths *ex* Harvey) Kützing, collected at Pineda Causeway, Rockledge (0.074 g dry/ml); data for *Elysia furvacauda* Burn (Brandley, 1984) were converted from displacement volume to dry weight using *Codium isthmocladum* Vickers from Sebastian Inlet (0.063 g/ml), and data for *Oxynoe antillarum* Mörch (Warmke and Almadovar, 1972) were converted from wet to dry weight using *Caulerpa racemosa* from Fort Pierce Inlet (0.051 g dry/g wet).

Ash weights were determined using oven-dried algae combusted in a muffle furnace at 500^{0}C.

Model II regression lines were calculated by Bartlett's three group method (Sokal and Rohlf, 1981).

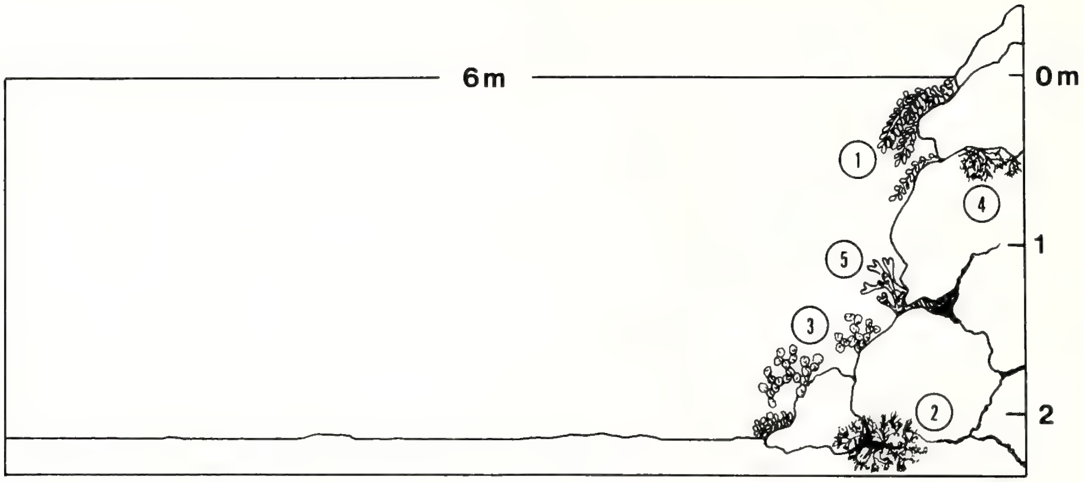
RESULTS

CARIBBEAN ASCOGLOSSAN HABITATS:

The known habitats of ascoglossans in the greater Caribbean province fall into several general types, and can be grouped on the basis of substrata (composition, grain size, and orientation), water quality (nutrient content, wave exposure or water flow), light level, and algal cover (which appears to relate strongly to the above characteristics). These habitat types are broadly distributed and have relatively similar ascoglossan faunae. The habitats are briefly described below, together with their characteristic ascoglossan species (Table 1). We indicate apparent (unmeasured) nutrient conditions based on color, clarity, and source of waters as: oligotrophic (tropical oceanic water of exceptional clarity); mesotrophic (estuarine or coastal water of slight turbidity, usually associated with well-oxidized sediments); eutrophic (water with visible tannin/humate content, sediments usually moderately to heavily organic, associated with mangrove drainage).

VERTICAL ROCK FACE *CAULERPA* ZONE (VRFC):

Common occurrences of this habitat (Fig. 4) include artificial jetties constructed as protection for navigation; natural equivalents also occur as nearshore fossil reefs from Sebastian Inlet, FL south to approximately Boca Raton, and at the outer margins of small bays in Bermuda. Waters are usually oligotrophic to slightly mesotrophic. *Caulerpa racemosa* is the dominant alga in this community, and typically occurs as a restricted band just below the low tide line, mixed with other algal species (most often *C. mexicana* (Sonder) Kutzing and *C. sertularioides* (Weber-van Bosse) Børgesen. Extent of this community can be limited by piscine herbivory, and the VRFC



Figs. 4-15. Representative habitats of Caribbean Ascoglossa. Some figures represent composites of several similar habitats (for specific occurrences of individual species, refer to Table 1). Some macrophytes are included for purposes of habitat description only, and are noted as "no ascoglossans". Macrophytes are not to scale. **Fig. 4.** Vertical Rock Face *Caulerpa*, High Energy (Sebastian Inlet, Fort Pierce Inlet, Bermuda Coastal Margins): 1 = *Caulerpa racemosa, C. sertularioides: Ascobulla ulla, Lobiger souverbiei* Fischer, *Oxynoe antillarum, Elysia subornata, Volvatella bermudae* Clark; 2 = *Cladophora prolifera* (Roth) Kützing: *Aplysiopsis zebra* Clark; 3 = *Halimeda discoidea: Elysia tuca, Bosellia mimetica, Cyerce antillensis;* 4 = *Bryopsis plumosa* (Hudson) C. Agardh: *Caliphylla mediterranea, Elysia ornata, Placida kingstoni* Thompson; 5 = *Codium: Placida* sp. (non *dentritica*).

is usually absent in coral reef areas. For example, in Bermuda, the rock faces at the south side of Castle Harbour are completely cleared of macrophytes by intense scarid grazing.

Sebastian Inlet: The winter low temperature apparently prevents establishment of *Halimeda*, but this is a significant component in more tropical examples of the VRFC. *Caulerpa* at Sebastian Inlet is strongly seasonal, usually disappearing from December through March, with a mid-summer dieback as salinity falls with summer rains (to below 20 $^0/_{00}$ after heavy rain). This habitat is restricted to the north inner jetty, perhaps by climatic effects or by extreme wave action and sediment abrasion on the outer jetties. The inner jetty is protected from heavy natural waves, but boat wakes generate frequent waves of low amplitude (1-3 dm) and there is a strong current (1-2 km/hr) for much of the tidal cycle.

Fort Pierce Inlet: Wave energy is more moderate here, and the *Caulerpa racemosa* belt extends into a sandy beach at the landward edge. There are protected tide pools, shaded and buffered against heavy surf, and these are also colonized by *Bryopsis*, with dense tufts of this alga in spring and after summer upwelling events (Smith, 1982). As previously noted (Jensen and Clark, 1983), this site contains the northernmost representatives of the tropical fauna, with *Elysia tuca* Marcus and *Ascobulla ulla* (Marcus and Marcus), *Bosellia mimetica* Trinchese, and the caliphyllids *Cyerce antillensis* Engel and *Caliphylla mediterranea* Costa; these have not been observed at Sebastian Inlet, about 50 km north. The more tropical nature of Fort Pierce is also evidenced by the occurrence of *C. racemosa* year-round in most years.

A series of fossil algal reefs parallels the shoreline at Ft. Pierce, and these appear to support a similar community. However, high wave energy has made exploration of these difficult.

Bermuda: The VRFC habitat occurs at the outer margins of small bays, with relatively sparse *Caulerpa* growth and qualitatively lower ascoglossan densities than Florida, and along the Bermudan causeways where there is strong current flow and somewhat higher animal densities (not quantified). There are also heavy growths of *C. racemosa* on the rock walls inside of Harrington Sound near submarine caves, associated with zones where groundwater from the caves mixes with seawater.

Florida Keys: Borrow pits (made by quarrying limestone, "borrowed" for highway construction) and marina canals commonly support variations of the VRFC community (Fig. 5). Borrow pits usually have restricted water exchange (with narrow inlets and flow only at high tide), no wave action, and a distinct thermocline is often present. When a thermocline exists, the bottom water is eutrophic and sometimes hypoxic; above the thermocline, where most opisthobranchs occur, the water is mesotrophic. *Caulerpa racemosa* grows in a looser, less compact form than in more exposed VRFC habitats, and a diverse and dense community of ophiuroids, polychaetes, anemones and other invertebrates is associated with the *Caulerpa* and rock crevices. *C. verticillata* is also a major component of these borrow pits and canals. High densities of *Tridachia crispata* Mörch occur in borrow pits and canals but are seldom associated with any particular alga.

Coral-Sand (CS): This habitat (Fig. 6) occurs where layers (2-40 cm) of carbonate sand usually overlie a limestone base, usually at depths of less than 2 m (the lower limit is usually bounded by a *Sargassum*/gorgonian zone). Sediments are typically coarse and well oxidized. Algal cover includes many of the genera of chlorophytes that are principal foods of ascoglossans, including *Halimeda, Udotea, Penicillus, Rhipocephalus, Avrainvillea,* and *Caulerpa.* Thicker sediment layers accumulate in local depressions in the limestone, and these are usually dominated by *Thalassia testudinum* Banks *ex* König; with decreasing sediment grain size and increasing organic content, seagrasses replace the algae, and the typical CS community appears as a mosaic of siphonalean algae and seagrasses. Slow to moderate water currents (<0.5 km/h) and oligotrophic to mesotrophic waters characterize these areas.

Upper Florida Keys: The best example of this community occurs at Point Elizabeth at the mangrove fringe, and supports a notably high diversity of ascoglossans at moderate densities.

Middle Florida Keys: Long Key, Spanish Harbor Key. Both sites are near bridges that cross channels, and these areas are well-flushed by tidal currents, especially Spanish Harbor (Fig. 6). High densities of *Elysia subornata* Verrill, *E. tuca*, and *E. papillosa* Verrill occur here seasonally (Table 2).

Lower Florida Keys (Big Pine Key, Geiger Key): Algae here are shorter and less densely spaced than at Key Largo, and animal densities are generally lower; however, this habitat supports the only known population of *Mourgona germaineae* Marcus and Marcus.

Ferry Reach, Bermuda: This area has finer sediments and a reduced algal diversity relative to the Florida Keys and Belize.

Blue Ground Range, Belize: This habitat occurs around many smaller cays among the Blue Ground Range, but densities of ascoglossans are very low except near

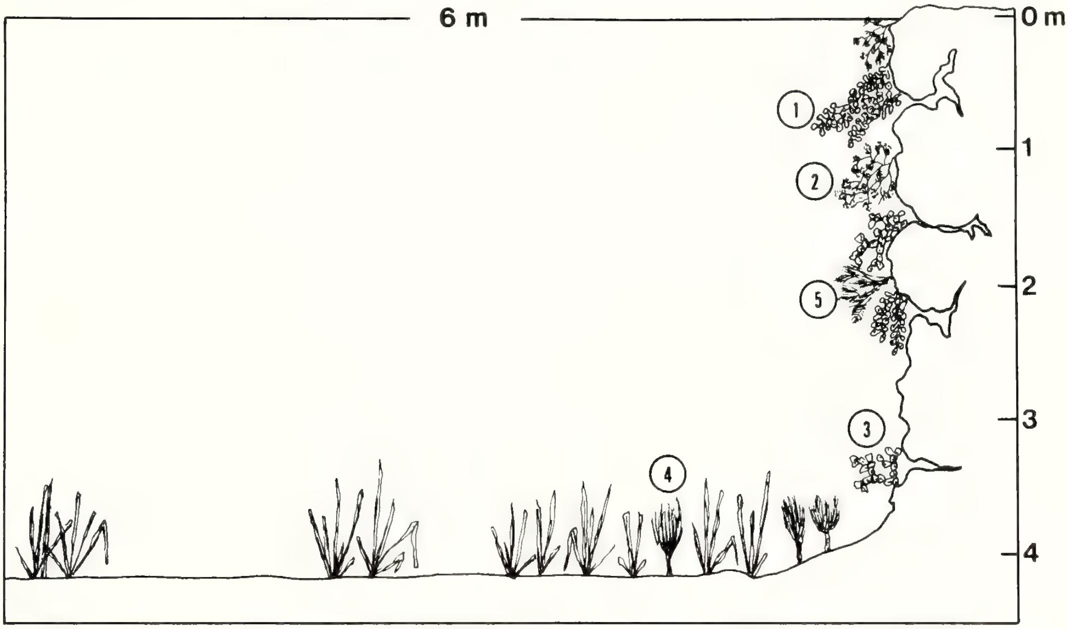


Fig. 5. Vertical Rock Face *Caulerpa*, Low Energy (Florida Keys Borrow Pits, Bermuda Causeways): 1 = *Caulerpa racemosa: Ascobulla ulla, Oxynoe antillarium, Elysia subornata, E. ornata;* 2 = *Caulerpa verticillata: Tridachia crispata* (juveniles), *E. subornata;* 3 = *Halimeda incrassata, H. discoidea: Bosellia mimetica, E. tuca;* 4 = *Penicillus dumetosus* (Lamouroux) Blainville: *Cyerce antillensis;* 5 = *Bryopsis: Placida kingstoni, Elysia ornata.*

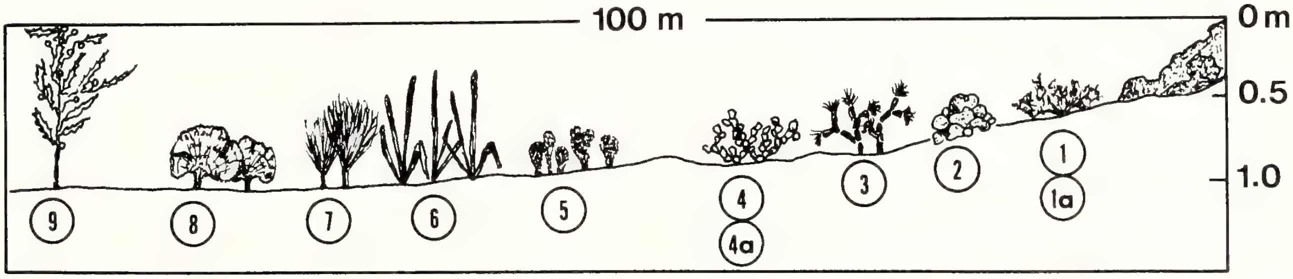


Fig. 6. Coral-sand (Point Elizabeth, Key Largo, FL; Long Key; Geiger Key; Spanish Harbor Key; Blue Ground Keys, Belize; Ferry Reach, Bermuda): 1 = *Cladophoropsis: Ercolania funerea, E. coerulea* Trinchese; 1a = *Caulerpa verticillata: Tridachia crispata;* 2 = *Dictyosphaera: Ercolania coerulea;* 3 = *Cymopolia barbata* (L.) Lamouroux: *Mourgona germainiae;* 4 = *Halimeda incrassata/H. discoidea: Elysia tuca, E. papillosa;* 4a = *Halimeda monile, H. tuna: Cyerce antillensis, Bosellia mimetica;* 5 = *Avrainvillea nigricans: Costasiella ocellifera* (Simroth), *C. nonatoi* Marcus and Marcus; 6 = *Thalassia testudinum: E. serca;* 7 = *Penicillus dumetosus: Elysia tuca, E. papillosa, Cyerce antillensis, E.* n. sp.; 8 = *Udotea conglutinata* (Ellis and Solander) Lamouroux: *E. papillosa;* 9 = *Sargassum* spp. (no ascoglossans); 10 = *Caulerpa paspaloides, C. cupressoides: E. subornata, Oxynoe azuropunctata* Jensen, *Lobiger souverbiei.*

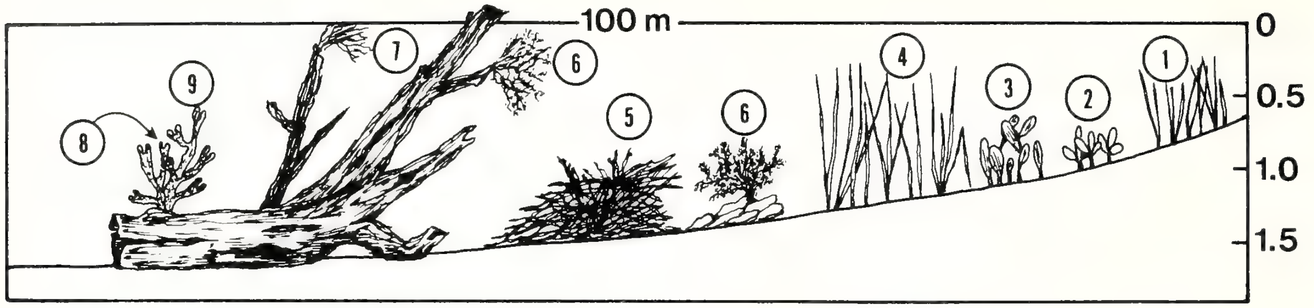


Fig. 7. Northern Indian River Lagoon: 1 = *Halodule wrightii* Ascherson: *Elysia serca;* 2 = *Halophila: E. serca;* 3 = *Caulerpa prolifera: E.* n. sp. "AF"; 4 = *Syringodium filiforme* Kützing (no ascoglossans); 5 = *Drift algal substrates (e.g. Acanthophora)—Chaetomorpha* sp.: *Ercolania funerea;* filamentous Rhodophyta: *Hermaea cruciata* Gould; 6 = *Bryopsis: Ercolania fuscata* (Gould), *Placida kingstoni, Cladophora* sp.: *Ercolania fuscata;* 7 = *Polysiphonia* sp.: *Ercolania fuscovittata* (Lance); 8 = Epiphytic diatoms (on *Codium*): *Elysia evelinae* Marcus; 9 = *Codium isthmocladium: Placida* sp., *Elysia canguzua* Marcus. Diet unknown: *E. chlorotica* Gould.

mangrove-colonized shorelines. Qualitatively, however, these areas are very similar to areas in the Florida Keys.

Man-O'War Cay, Belize: This small mangrove cay is a rookery; the water up to 50 m from the island has an odor of guano, suggesting a high nutrient content. There is a rich growth of *Bryopsis* extending from below the mangroves to about 40 cm depth, followed by a dense meadow of *Caulerpa racemosa* to about 1 m. In June 1985, we found a great mass of *Chaetomorpha*, estimated at a volume of 23 m^3, containing a total of four *Ercolania funerea* (Costa).

SUBTROPICAL BARRIER-ISLAND LAGOON: In subtropical Florida, barrier islands enclose a long salt lake, the Indian River Lagoon. In its undisturbed state, examples of which are unfortunately disappearing rapidly, the Indian River Lagoon received most nutrient input via a very restricted watershed and very limited oceanic exchange, with production dominated by seagrasses and apparently a near-equilibrium of production and respiration. The balance of production and respiration is evidenced by a fine silica sand bottom of low organic content (Gilbert and Clark, 1981). Currents are slow and wind driven except near inlets (von Zweck and Richardson, 1980). Temperature varies widely and rapidly on both diurnal and seasonal scales because of the high surface area: depth ratio of the lagoon (Smith, 1983). Salinity varies with rainfall, and is highest at the end of the dry season. In recent years, much of the lagoon has moved toward a high-turbidity system with increased nutrient influx accompanying urbanization and agricultural expansion, and the seagrasses are steadily declining.

The ascoglossans of the northern Indian River Lagoon (Sebastian to Haulover Canal) are represented in Fig. 7, a composite of species observed since 1972 in this habitat. Two significant changes have occurred during this period; in the absence of prior data, we are unable to determine whether these are permanent or cyclic changes. From 1972 to about 1976, *Chaetomorpha* was a dominant alga in the lagoon and was heavily colonized by *Ercolania funerea* (Costa); at the Haulover Canal in Titusville in 1973, for example, we were able to collect thousands of slugs simply by scooping handfuls of algae into a bucket. In later years, however, the abundance of the alga steadily declined and today the alga occurs as only as isolated threads and small clumps in drift algal masses in most of the areas where it was formerly abundant. A second noteworthy change is the colonization of the North Indian River by *Caulerpa prolifera* (Forsskål) Lamouroux circa 1980. Absent from this part of the river in 1975 (Gilbert and Clark, 1981), *C. prolifera* now forms patches in the sandy bottom at a depth of about 0.5-1.0 m; an undescribed *Elysia*, morphologically similar to *E. subornata* Verrill, eats this alga and occurs from Sebastian to Titusville.

MANGROVE CHANNEL FLOOR (MCF): This habitat occurs in mature mangrove areas in which channels have eroded the peat foundation, sometimes producing a soft, organic mud/silt substrate; waters are mesotrophic to highly eutrophic, depending upon the extent of mangrove drainage. In the best-developed MCF habitats, mature mangrove canopy provides partial or complete shading, and the extent of drainage produces a moderate tidal flow; in some locations, a sand bottom could be present. The peat walls of the channel often support growth of *Caulerpa verticillata.*

Key Largo, Lake Surprise (Fig. 8): Drainage from mangrove areas feeds through Jewfish Creek and into a tidal roadside canal; this canal empties into the Lake Surprise Lagoon onto a delta about 1 m deep. Sediments are partly organic, partly calcareous silt with some shell chaff. *Caulerpa paspaloides* and *Halimeda incrassata* (Ellis and Solander) Lamouroux dominate in patches between the mangrove fringe and the *Thalassia* beds; "islands" of dense patches (1 m diameter) of *Avrainvillea nigricans* Decaisne occur near the mangrove fringe. The roadside canal itself is colonized by some *Thalassia* and *Penicillus*, but like the Twin Cays channel floors described below, has a depauperate ascoglossan fauna, possibly because of the high silt load. A well-developed epimanglic community is present at the mangrove fringe, described separately below.

Twin Cays, Belize, Main Channel (Fig. 9). In broader parts of the channel, the sediment is fine calcareous sand/silt. The diversity of algae and slugs is low here, and densities were too low to sample.

Twin Cays, Hidden Creek (Fig. 10): Sediment here is

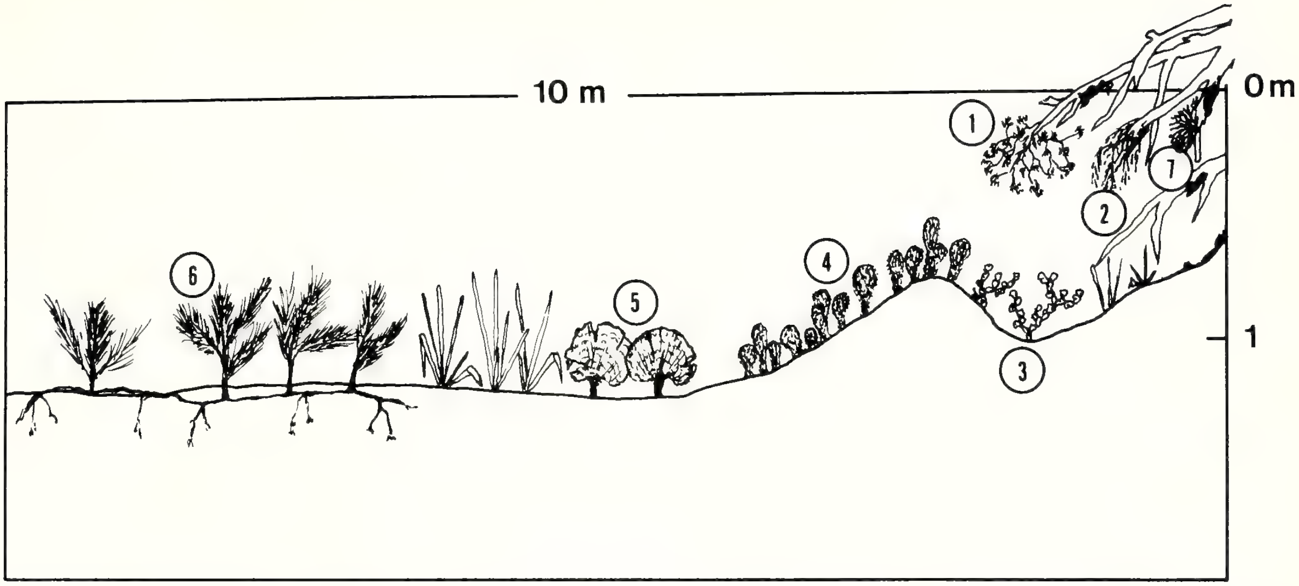


Fig. 8. Mangrove Fringe, Lake Surprise, Key Largo, Florida (Epimangle, Tidal Canal, Mangrove Channel Floor and Delta): 1 = *Caulerpa verticillata: Elysia subornata;* 2 = *Cladophoropsis* sp.: *Ercolania funerea;* 3 = *Halimeda incrassata: Elysia tuca;* 4 = *Avrainvillea nigricans: Costasiella ocellifera;* 5 = *Udotea conglutinata: Elysia patina;* 6 = *Caulerpa paspaloides: Oxynoe azuropunctata, Elysia subornata, Ascobulla ulla;* 7 = filamentous Rhodophyta: *Hermaea cruciata.*

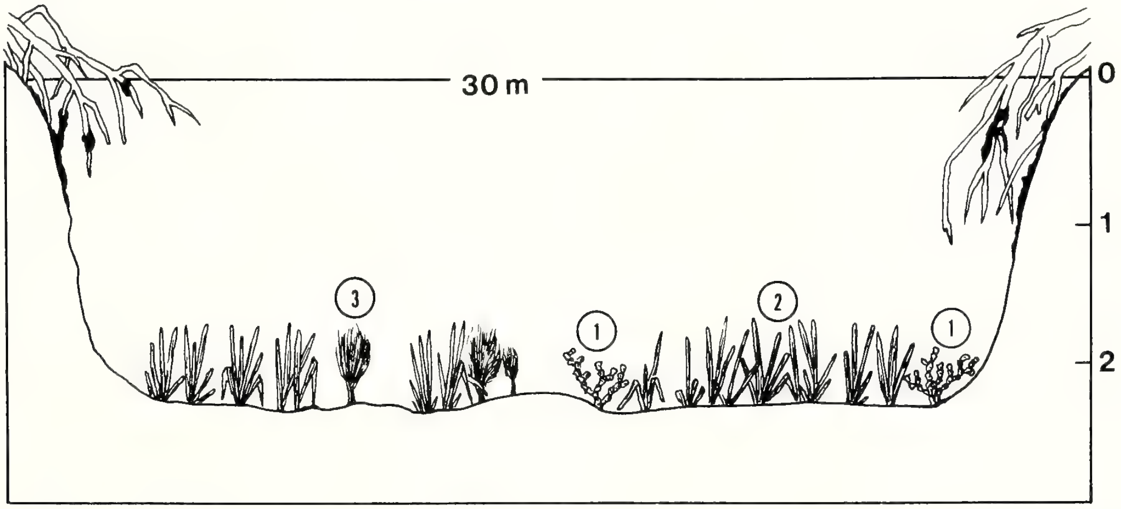


Fig. 9. Mangrove Channel Floor, Twin Cays Main Channel, Belize: 1 = *Halimeda incrassata: Elysia tuca;* 2 = *Thalassia testudinum: Elysia serca;* 3 = *Penicillus capitatus* Lamarck: not colonized.

soft, flocculent, and highly organic. The water is rich in dissolved organic matter draining from shallow mangrove areas in the interior of the island, and reaches high temperatures (34°C in June 1985) if tides ebb in late afternoon. As in the main channel, algae of the channel floor are sparsely colonized, except at ridges at the mouth of the channel, or in patches of algae located at channel junctions.

CHANNEL EPIMANGLE (EPM): Buttress-roots of *Rhizophora mangle* L. extend along the banks of mangrove channels, at times to a depth of >1 m. These buttresses support dense growths of *Caulerpa* just below the surface, particularly where partially shaded by the *Rhizophora* canopy (Fig. 10). Algae here are isolated from most silt of the channel floor, and support a diverse and moderately dense community of ascoglossans. Optimal conditions appear to occur in narrow, deep channels with high flow and complete shading, as in Hidden Creek and Grouper Garden Channel, Twin Cays. This habitat is poorly represented in most of the Florida Keys, where mangroves are often more fringing growths in shallow water and there is a poor development of epimanglic algae.

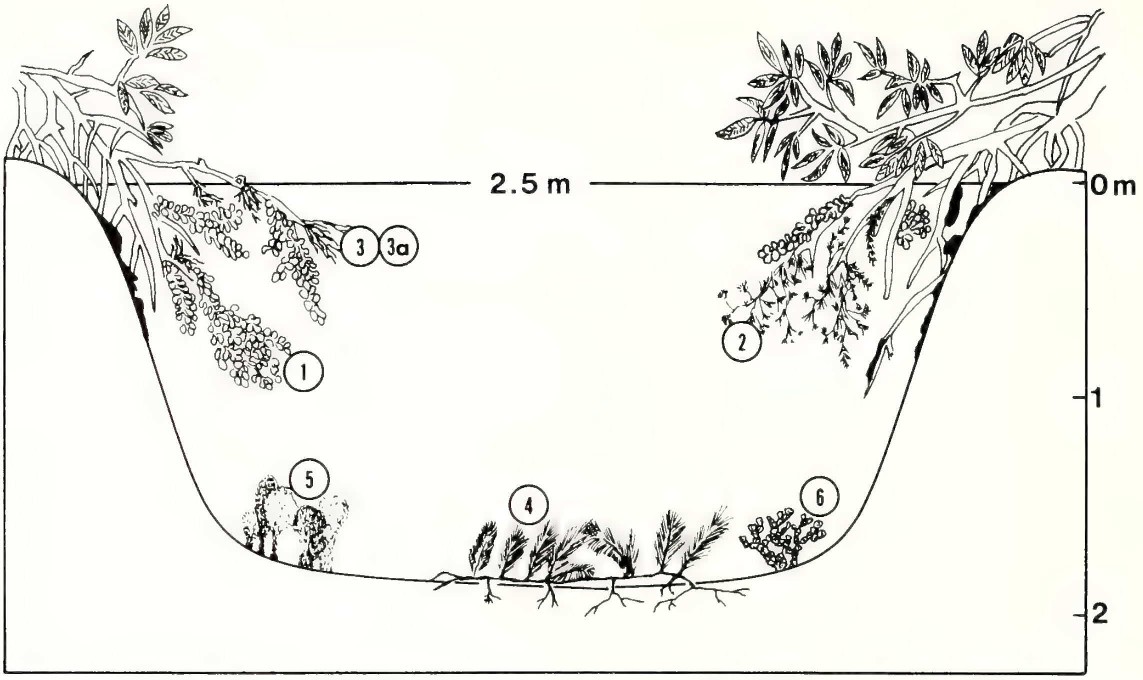


Fig. 10. Mangrove Channel Epimangle and Channel Floor (Twin Cays—Hidden Creek, Grouper Garden): 1 = *Caulerpa racemosa: Elysia subornata, Ascobulla ulla, Volvatella bermudae, Lobiger souverbiei;* 2 = *Caulerpa verticillata: Berthelinia caribbea* Edmunds; 3 = *Cladophoropsis: Ercolania coerulea:* 3a = *Bryopsis: Placida kingstoni;* 4 = *Caulerpa paspaloides: Oxynoe azuropunctata;* 5 = *Avrainvillea nigricans: Costasiella ocellifera;* 6 = *Halimeda* spp.: *Bosellia mimetica.*

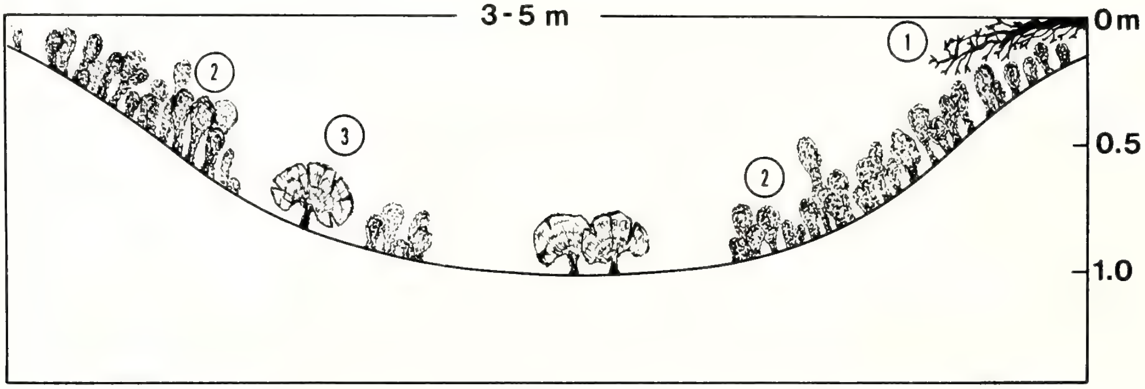


Fig. 11. Mangrove Pond Floor, Twin Cays: 1 = *Acanthophora spicifera* (Vahl) Børgesen (no ascoglossans); 2 = *Avrainvillea nigricans: Costasiella ocellifera, C. nonatoi; Udotea conglutinata: Elysia patina, E. subornata.*

MANGROVE POND FLOOR (MPF): Twin Cays (Fig. 11): In the interior of Twin Cays, broad, shallow ponds (50-100 m x <0.5 m) form at the end of major channels, apparently via decomposition of mangrove peat. The bottoms of these are largely decomposed peat, but some sandy patches occur. There are sparse patches of *Avrainvillea* and *Udotea*, but high densities (Table 2) of ascoglossans occur on these algae.

BACK REEF FLAT/REEF CREST (BRC): The substrate here is limestone with a thin layer of sediment localized in depressions; water is oligotrophic and a nearly constant flow crosses the BRC. Algal growth is dense, but often closely cropped by fish, especially the uncalcified algae (e.g. *Caulerpa* spp.), and forms an algal turf in areas near the leeward reef crest (Lewis, 1985).

Southwater Cay, north end (Fig. 12): The reef crest here is broader than at Carrie Bow Cay and the back reef is deeper (2-3 m), with higher densities of slugs.

Carrie Bow Cay (Fig. 13): Much of the back reef flat here is quite shallow (<0.5 m in most areas) and exposed to surf for part of each tidal cycle. Most of the ascoglossans here feed upon *Halimeda* spp.; *Elysia serca* Marcus is ap-

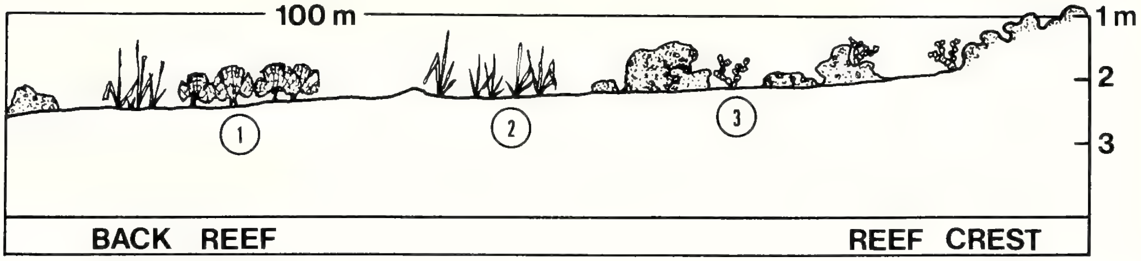

100 m
1 m
2
3
1
2
3
BACK REEF
REEF CREST

Fig 12. Back reef/reef crest, Southwater Cay, Belize: 1 = *Udotea conglutinata: Elysia papillosa, E. tuca;* 2 = *Thalassia testudinum: Elysia serca;* 3 = *Halimeda incrassata: E. tuca, Elysia* n. sp.

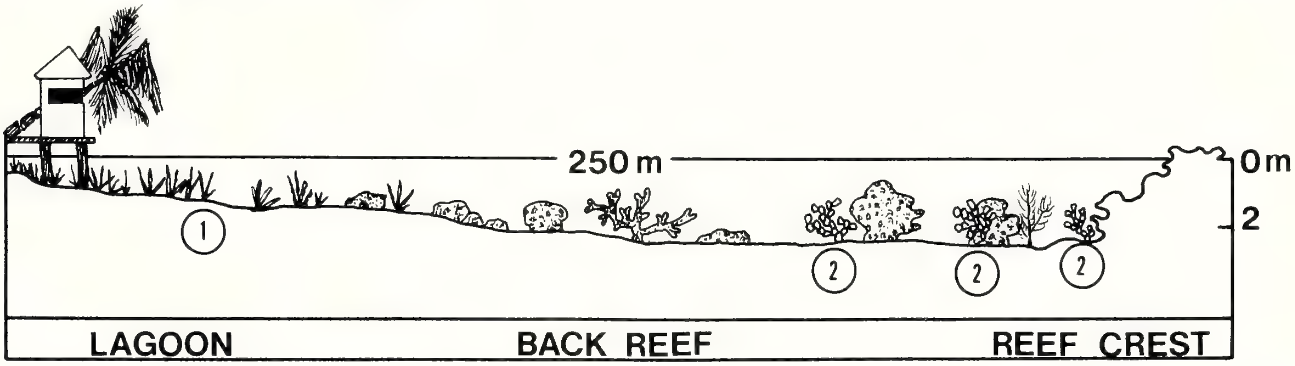

250 m
0 m
2
1
2
2
2
LAGOON
BACK REEF
REEF CREST

Fig. 13. Back Reef Flat/Reef Crest, Carrie Bow Cay, Belize: 1 = *Thalassia testudinum:* no animals; 2 = *Halimeda* spp.: *Elysia tuca, E. flava, Tridachia crispata, Elysia* n. sp., *Bosellia mimetica.*

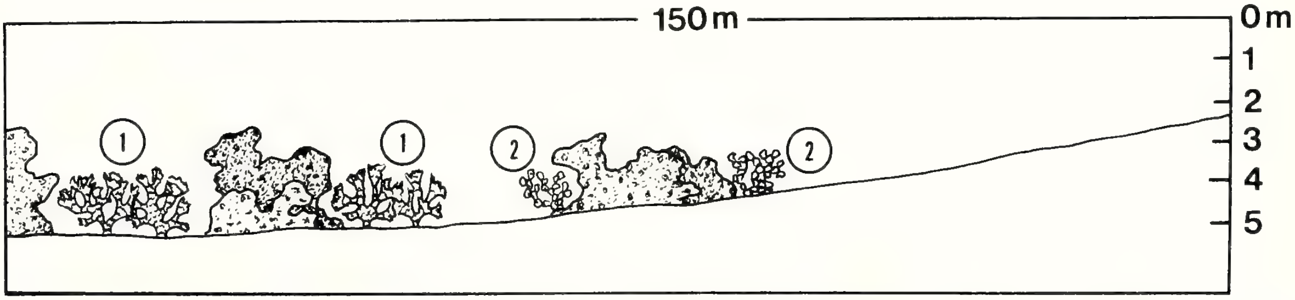

150 m
0 m
1
2
3
4
5
1
1
2
2

Fig. 14. Curlew Bank Back Reef, Belize: 1 = *Stypopodium zonale* (Lamouroux) Papenfuss (epiphytes): *Elysia tuca, E. papillosa;* 2 = *Halimeda incrassata: Elysia tuca, E. subornata, Bosellia mimetica.*

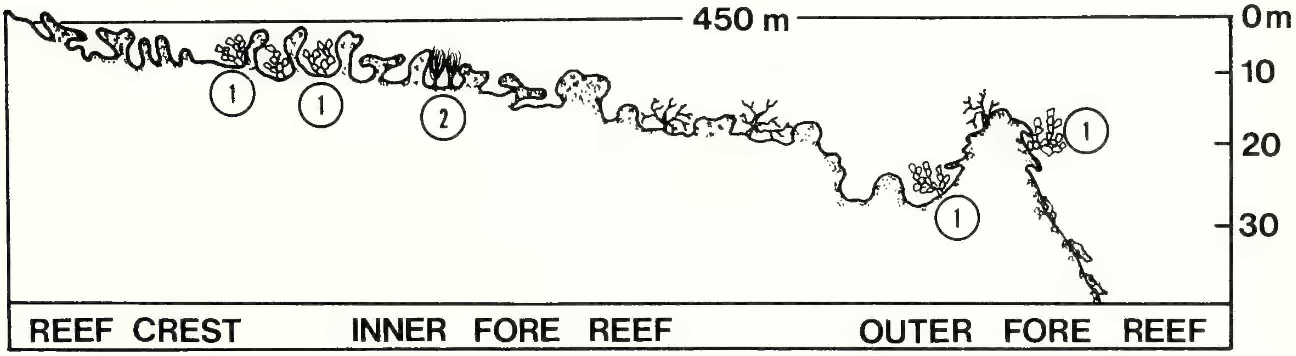

450 m
0 m
10
20
30
1
1
2
1
1
REEF CREST
INNER FORE REEF
OUTER FORE REEF

Fig. 15. Reef Crest, Inner Fore Reef, and Outer Fore Reef, Carrie Bow Cay, Belize: 1 = *Halimeda discoidea, H. Simulans* Weber-van Bosse: *Bosellia mimetica, Elysia flava, Elysia* n. sp. "BL", *Tridachia crispata, E. papillosa;* 2 = *Penicillus dumetosus: Cyerce antillensis, E. papillosa.*

parently absent from the *Thalassia*, possibly due to strong currents.

Deep Back Reef, Curlew Bank: The reef crest at this site has eroded, and the back reef slopes rapidly to about 5 m depth (Fig. 14). Two *Elysia* species are associated with the dominant alga *Stypopodium*, apparently feeding on a fine growth of epiphytes on the surface of this alga; these slugs occur in moderate densities but we were unable to quantitatively sample these because of the difficulty of separation of epiphytes from *Stypopodium* thalli. The sand/rock bottom supports few macrophytic chlorophytes other than *Halimeda incrassata*.

Fore Reef/Reef Slope, Carrie Bow Cay (Fig. 15): Algae in this zone are primarily epilithic, with little sediment available for rhizoid attachment. Animal densities are notably lower here, with samples from the fore reef slope below measurable density in most places. Samples from the slope, examined in the laboratory, often had moderate numbers of *Bosellia* juveniles, but these were not quantified.

HABITAT COMPARISONS

Habitats investigated in this study are compared in a trellis diagram based on similarity coefficients (Fig. 16). In general, these habitats are quite distinct, with most associations sharing less than 75% of their species. Three of the Belizean communities are the most distinct (<30%), apparently because the number of species in these habitats (mangrove pond floor, coral-sand, and fore-reef slope) is very low relative to most other communities. The Indian River Lagoon is also quite distinct (32% similarity) from other Caribbean communities, reflecting the presence of several temperate species absent from other Caribbean habitats. The greatest similarity is shown by communities of similar type separated by short distances (Largo and Geiger CS, and Bermuda coastal and causeway VRFC).

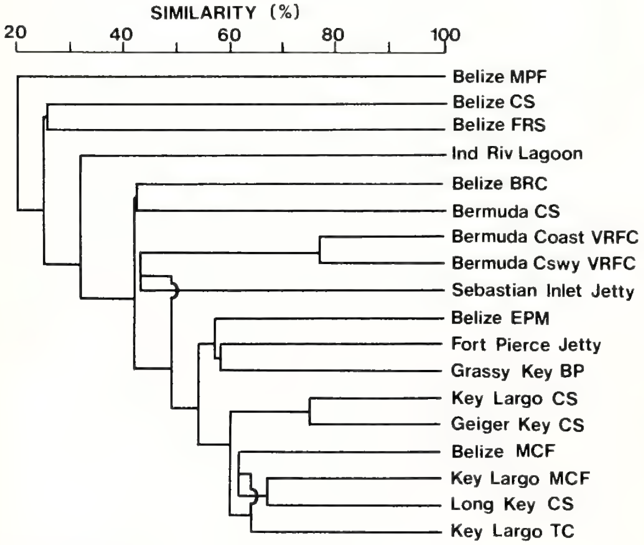


Fig. 16. Trellis diagram of similarity of Caribbean ascoglossan communities. Abbreviations: MPF: mangrove pond floor; CS: Coral-sand; FRS: fore-reef slope; LBRC: back reef/reef crest; VFRC: vertical rock-face *Caulerpa*; EPM: epimangle; BP: borrow pit; MCF: mangrove channel floor; TC: tidal canal.

Most ascoglossans appear to be highly specialized in habitat selection, with about three-fourths of the species occurring in less than thirty percent of the habitats studied (Fig. 17).

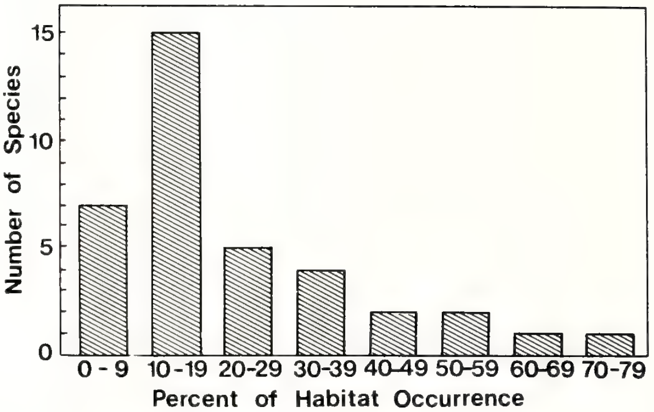


Fig. 17. Habitat selectivity of Caribbean ascoglossans among fifteen habitats.

FAUNAL DENSITIES AND BIOMASS RATIOS:

Densities (animals per unit of algal biomass) and biomass ratios (total animal weight per unit algal weight) are summarized in Table 2. Peak density strongly correlates with latitude when all species are grouped (Fig. 18).

The two major subgroups of the data set, elysiids and stiligerids, were further compared by analysis of covariance (ANCOVA). Residual variance ($F = 1.55$) and slopes ($F = 0.76$) of the two families did not significantly differ, but intercepts of the two groups did differ ($F = 9.34$; d.f. = 1, 16; $p<.01$). However, at the sample size of the stiligerid and elysiid data subsets, the relationships between density and latitude are not significant (stiligerids: $r = .59$ with 9 d.f.; elysiids: $r = .59$ with 6 d.f.).

Higher densities were found in Belizean mangrove habitats than in reef habitats (log transformation; Student's $t = 1.79$ with 12 d.f., $p<.05$; mean mangrove density = 0.218/g; mean reef density = 0.028/g). The mean biomass ratio of mangrove areas (0.00178) was greater than that of reef areas (0.00085) but the difference was not significant (log transformation; $t = 0.70$ with 10 d.f.).

Differences in species composition of the mangrove and reef areas are also distinct (Table 1), with 17 species in the combined mangrove habitats (mangrove channel floor, epimangle, and mangrove pond floor) and eight species in the combined back reef/fore reef; only five species co-occur in both mangrove and reef areas (*Tridachia crispata, Elysia subornata, E. tuca, Bosellia mimetica, Cyerce antillensis*).

Peak biomass ratios increased with latitude (Fig. 19), indicating that high-latitude algae support higher standing stocks of ascoglossan slugs than do more tropical algae. An

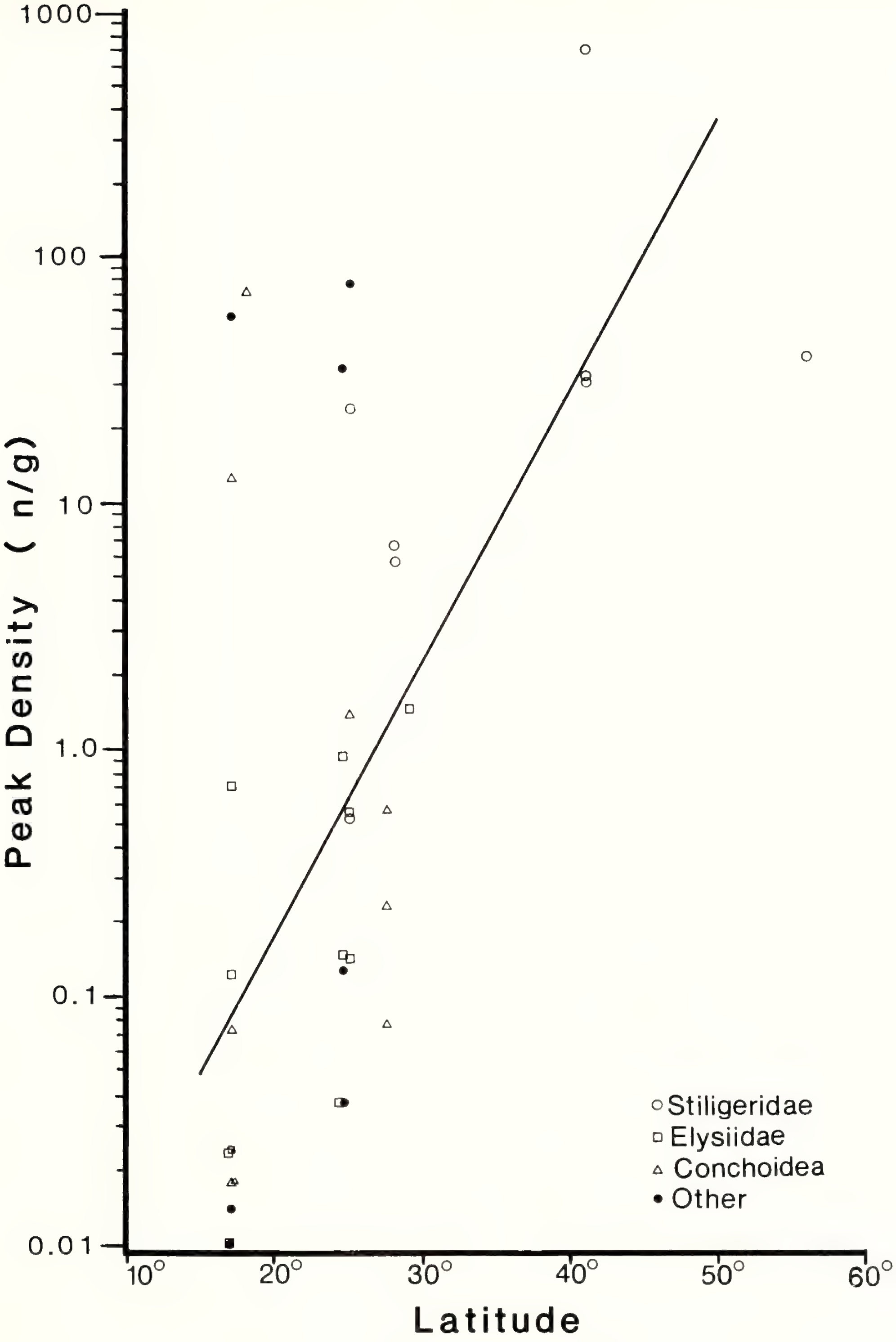


Fig. 18. Relationship of latitude and peak densities (n g^{-1} dry wt) of north Atlantic ascoglossan populations: Log_{10} (density) = 0.1109 (latitude) -2.9683, with r = .65; the relationship is highly significant ($p < .01$) with 33 degrees of freedom.

ANCOVA for comparison of the two major subgroups (elysiids and stiligerids) indicated that the residual variance was not significant (F = 3.49, d.f. = 1, 5), permitting comparison of separate subgroups. Slopes (F = 3.71, d.f. = 1, 11) and intercepts (F = 0.003, d.f. = 1, 12) of the two subgroups did not differ significantly, however.

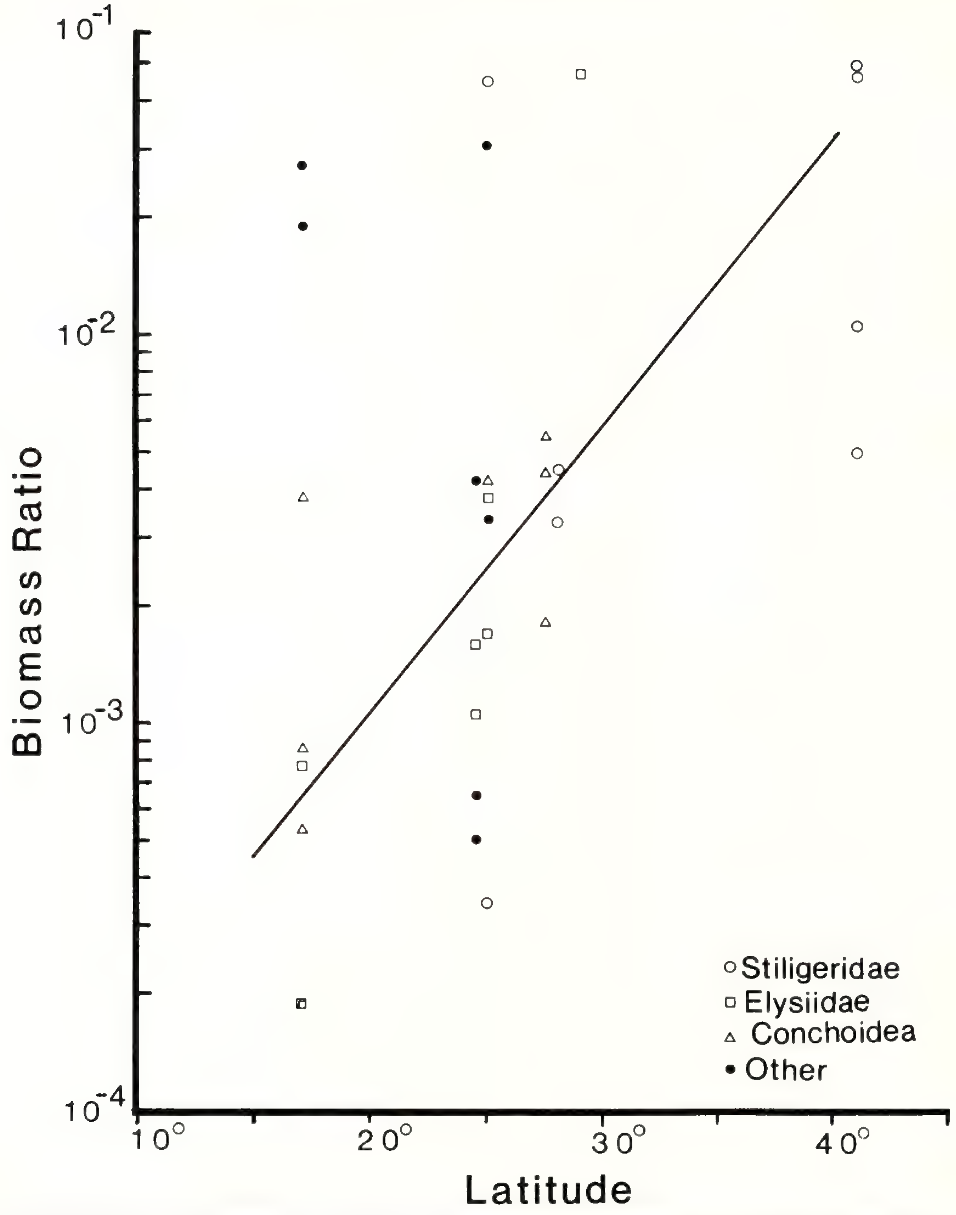


Fig. 19. Relationship of latitude and biomass ratio (dry weight of slugs: dry weight of algae) of north Atlantic ascoglossan populations: Log$_{10}$ (biomass ratio) = 0.0744 (latitude) - 4.449, with r = .535; the relationship is highly significant ($p < .01$) with 28 degrees of freedom.

Peak densities and algal ash level correlated strongly and inversely (Fig. 20), with nearly a 1000-fold range in density. Densities were generally highest in mangrove habitats and lowest in reef areas (Table 2). A similar effect was observed for biomass ratio and algal ash level (Fig. 21), but a narrower range of values suggests that differences in animal size (smaller animals on low-ash algae) can affect biomass ratios.

DISCUSSION

Ascoglossans' life histories are strongly entrained upon those of their algal foods (Clark, 1975). Consequently, their populations occur as a spatial and temporal subset of the occurrences of their algal foods, which are themselves often quite habitat-specific. This generates a highly "clumped" distribution for many species, in which relatively small populations occur, scattered within a very small percentage of the area of a potential habitat. These patterns of occurrence make quantitative sampling difficult, because the principle of fully-randomized population sampling is difficult to apply in the analysis of strongly disjunct, low-density populations. Consequently, the probability of collecting even a few slugs by standard marine sampling protocols is very small. Ascoglossans rarely appear in general community analysis tabulations, and when they do, occur as minor com-

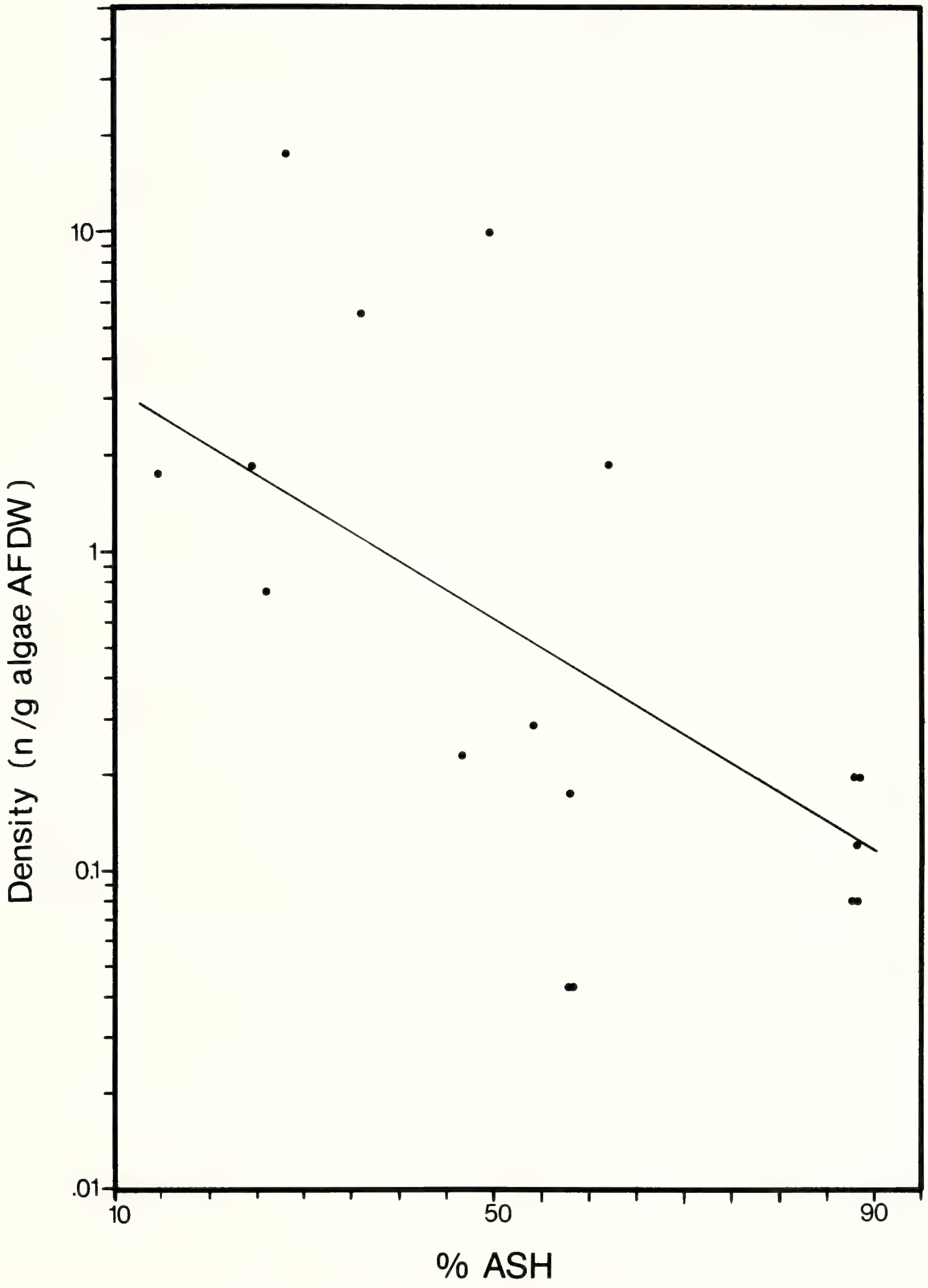


Fig. 20. Relationship of peak densities of Caribbean ascoglossans and algal ash level: Log_{10} (density) = -.01826 (%Ash) + .7002 with r = -.644; the relationship is highly significant ($p < .01$) with 15 d.f.

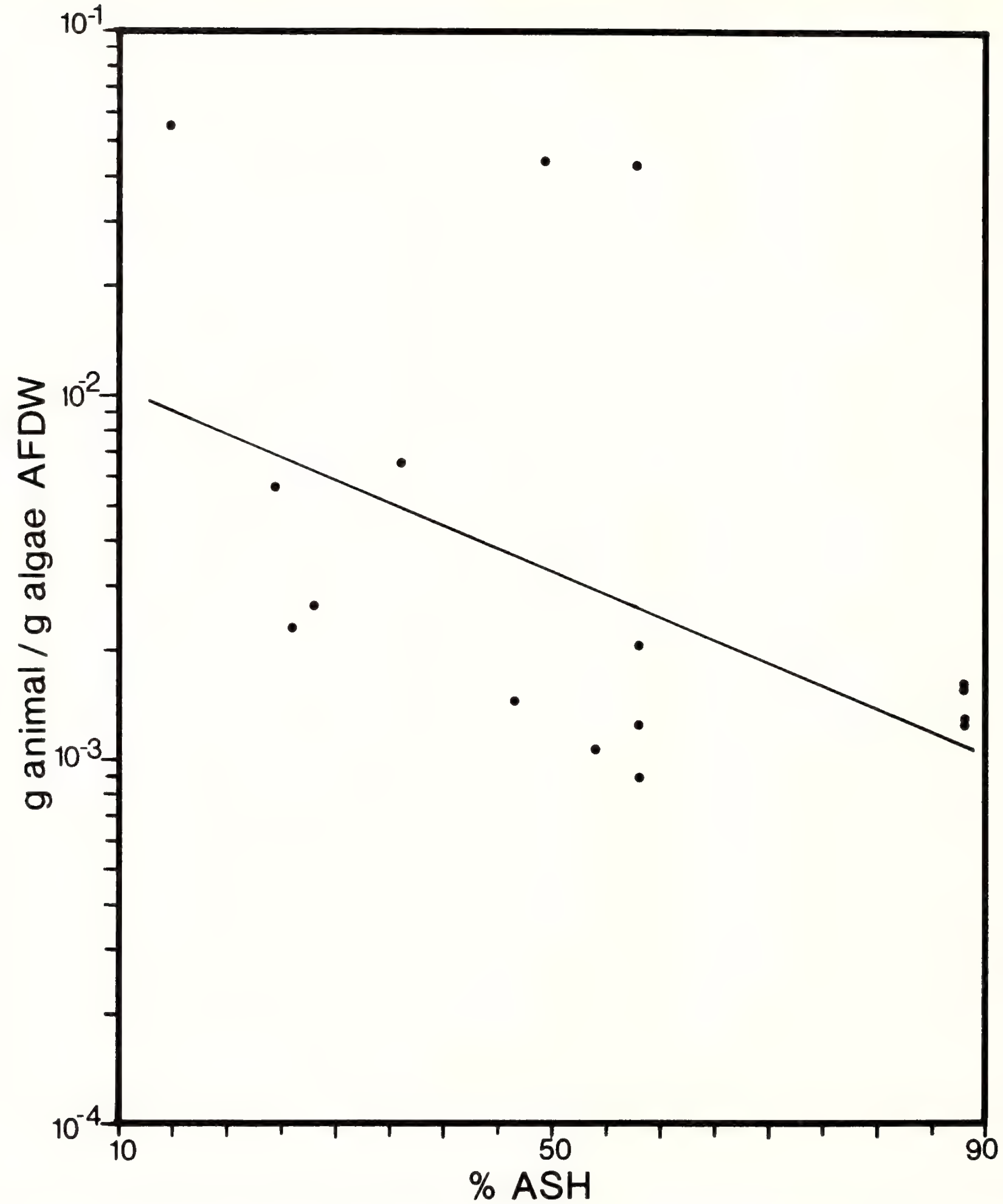


Fig. 21. Relationship of biomass ratio (dry weight of slugs/algal ash-free dry weight) and algal ash level for Caribbean ascoglossan populations: Log_{10} (biomass ratio) = -.01256 (% Ash) - 1.8649, with r = .561; the relationship is significant ($p < .05$) with 13 d.f.

ponents (e.g. Marsh, 1973).

There are distinct differences in the composition, population density, and diversity of Caribbean ascoglossan communities. Because ascoglossans are highly stenotrophic, the habitat is defined primarily by the algae present, which presumably vary with such environmental factors as type of substratum and nutrient availability. Ascoglossans, however, seem to be more sensitive to some environmental parameters than are their host algae, because the same algal species can occur in different communities with different ascoglossans predators (though the reverse is seldom true), and suitable foods often occur without ascoglossan predators. There are also substantial within- and between-habitat population differences (density and biomass ratios) of ascoglossan species on the same algal species. Climatic effects also contribute to faunal differences, as shown in comparison of the *Caulerpa racemosa* communities at different latitudes. Thus, ascoglossan populations potentially serve as sensitive environmental indicators.

Factors that affect ascoglossan populations can best be defined via analysis of quantitative population differences and covariant environmental variables. In this study, two

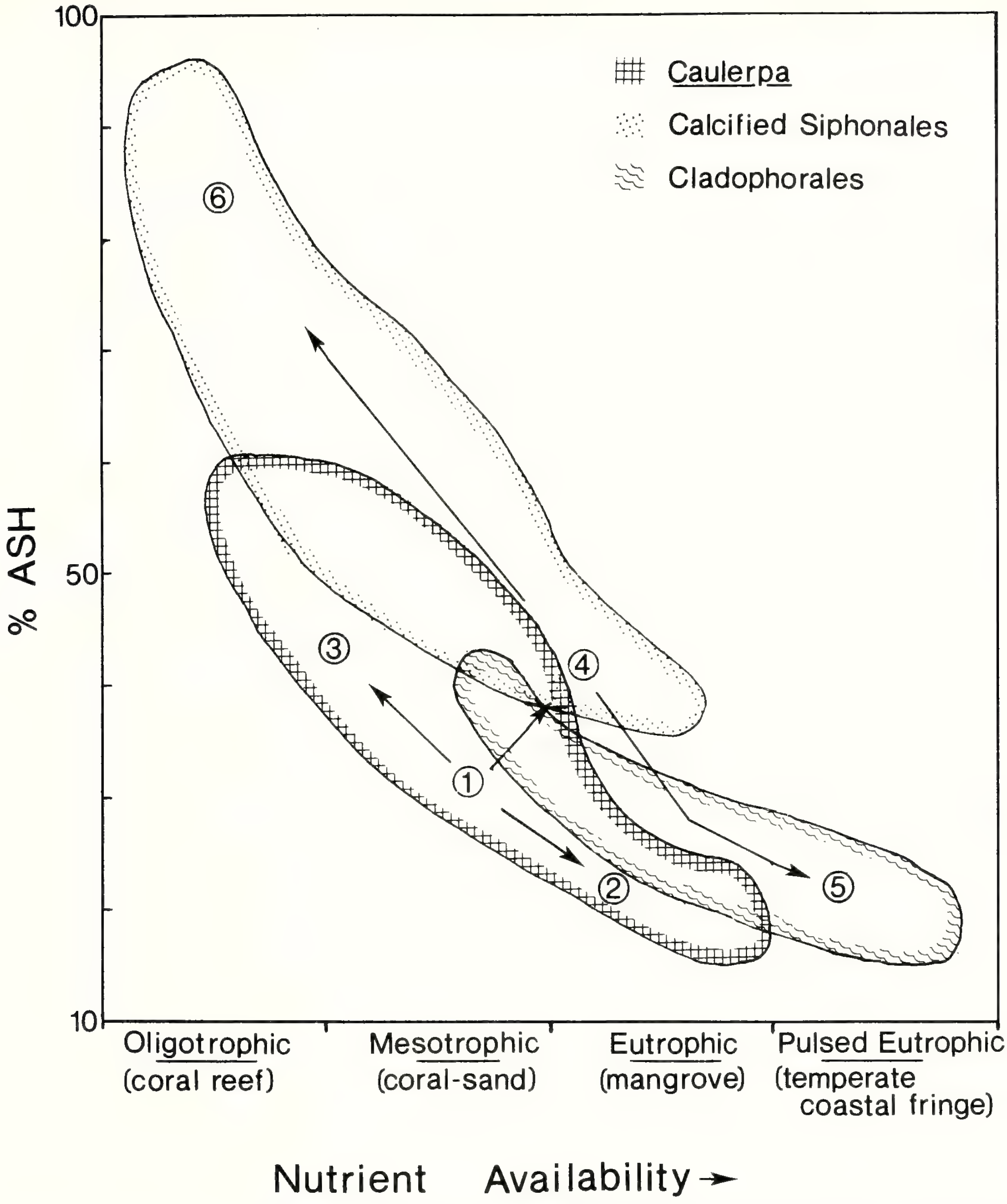

100
50
10
% ASH
Caulerpa
Calcified Siphonales
Cladophorales
⑥
③
④
①
②
⑤
Oligotrophic (coral reef)
Mesotrophic (coral-sand)
Eutrophic (mangrove)
Pulsed Eutrophic (temperate coastal fringe)
Nutrient Availability→

Fig. 22. Conceptual diagram of possible ascoglossan evolution in relation to feeding groups and habitats. 1 = niche of primitive burrowing Conchoidea; 2 = epimanglic Conchoidea; 3 = epilithic and reef-dwelling Conchoidea; 4 = initial adaptive radiation of unshelled ascoglossans in mangrove fringe and coral-sand habitats; 5 = radiation to Cladophorales via epimanglic filamentous algae; 6 = calciphilic radiation of elysiids, caliphyllids, and boselliids on high-ash *Halimeda* in reef systems.

variables, latitude and algal ash content, significantly correlated with variation in ascoglossan populations. Both ash content and latitude exhibit interesting possible relationships with higher taxonomic levels of the Ascoglossa and with algal morphology and taxonomy. These relationships, as discussed below, appear to provide a broad framework for consideration of the major evolutionary trends among ascoglossan families.

FUNCTIONAL ALGAL/ASCOGLOSSAN ASSOCIATIONS:

Molluscan herbivores have been grouped as "func-

Table 1. Occurrence of ascoglossan species in Caribbean habitats. 1 = occurrence of species in habitat, 0 = absence. Habitat abbreviations (in order of presentation): Indian River Lagoon, FL; Sebastian Inlet Jetty, FL; Fort Pierce Jetty, FL; Bermuda Coastal Vertical Rock Face; Bermuda Causeways; Bermuda Coral-sand; Grassy Key Borrow Pit, FL; Key Largo Tidal Channel, FL; Key Largo Mangrove Channel Floor, FL; Long Key Coral-Sand, FL; Geiger Key Coral-sand; Belize Mangrove Channel Floor, Twin Cays; Belize Mangrove Pond Floor, Twin Cays; Belize Epimangle, Twin Cays; Belize Back Reef Crest; Belize Back Reef Crest; Belize Fore Reef Slope; Belize Coral-sand.

Species	Ind Riv Lag	Seb Inl Jtty	Ft Pier Jtty	Bda Cst VRF	Bda Csy VRF	Bda CS	Gras Key BP	Lar go TC	Lar go CS	Lar go MCF	Lng Key CS	Gei ger CS	Bel ize MCF	Bel ize MPF	Bel ize EPM	Bel ize BRC	Bel ize FRS	Bel ize CS	Total habitats	% habitats
Ascobulla ulla (Marcus and Marcus)	0	1	1	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	8	0.44
Berthellinia caribbea Edmunds	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	2	0.11
Lobiger souverbiei Fischer	0	1	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	7	0.39
Oxynoe antillarum Mörch	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	8	0.44
O. azuropunctata Jensen	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	4	0.22
Volvatella bermudae Clark	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0.17
Bosellia marcusi Marcus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.06
B. mimetica Trinchese	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	6	0.33
Caliphylla mediterranea Costa	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
Cyerce antillensis Engel	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	1	0	1	9	0.50
C. crystallina (Trinchese)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
Mourgona germaineae Marcus and Marcus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.06
Costasiella nonatoi Marcus and Marcus	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0.11
C. ocellifera (Simroth)	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	7	0.39
Elysia evelinae Er. Marcus	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0.11
E. canguzua Er. Marcus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.11
E. chlorotica Gould	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
E. flava Verrill	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	4	0.22
E. ornata Swainson	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.17
E. papillosa Verrill	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	0	5	0.28
E. patina Ev. Marcus	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	3	0.17
E. serca Er. Marcu	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	5	0.28
E. sp. "BL"	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0.11
E. sp. "AF"	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
E. sp. "GN"	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.11
E. sp. "ST"	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	3	0.17
E. subornata Verrill	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	13	0.72
E. tuca Marcus and Marcus	0	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1	0	1	12	0.67
Tridachia crispata Mörch	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	10	0.56
Ercolania coerulea Trinchese	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	4	0.22
E. funera (Costa)	1	1	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	7	0.39
E. fuscata (Gould)	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0.11
E. fuscovittata (Lance)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.11
Placida kingstoni Thompson	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.17
P. sp. "CD"	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0.22
Hermaea cruciata Gould	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0.11
Aplysiopsis zebra Clark	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.06
Diversity	10	8	14	5	9	10	10	13	13	7	7	11	6	4	10	8	3	5		

tional groups" (groups of functionally similar species of broadly similar diet), but opisthobranchs have been excluded because of inadequate information on diet and ecology (Steneck and Watling, 1982). Ascoglossans form functional groups distinct from those previously recognized.

There are three major functional types of algae utilized by most Caribbean Ascoglossa. These types appear to be adapted to different nutrient regimes, which affect algal morphology and life history. Algal morphologies and life histories in turn have shaped the evolution of major ascoglossan groups at the family level.

Jensen (1983) previously noted that dietary preferences are partly shaped by algal thallus diameter. This partially reflects nutrient regimes, with more finely filamentous algae occurring in mangroves, high-energy environments, or temperate areas. Filamentous structure in these algae appears to permit rapid uptake of water column nutrients via high surface-volume ratio. Other dietary differences include presence or absence of septa, algal cytoplasmic viscosity (siphonalean algae have latex-like cytoplasm, which coagulates on contact with sea water) and ash level.

The Ascoglossa originated on species of *Caulerpa* (Kay, 1968) and adaptively radiated in two directions, one utilizing ephemeral algae (represented primarily by Cladophorales), and the other utilizing primarily non-caulerpan Siphonales (Clark and Busacca, 1978). These radiations coincide well with gradients of nutrients and ash level (Fig. 22).

Species of *Caulerpa* are pseudoperennial (individual thalli live less than one year, but the plant as a whole is long-lived). *Caulerpa* species are intermediate in ash content (15-60%), coenocytic, almost wholly tropical, and occur predominantly in mesotrophic environments on a variety of substrata, including rock, mangrove roots, and sediments that range from organic silts to well-oxidized sand. *Caulerpa* species have well-developed absorptive rhizoids that either penetrate sediment or, in epilithic/epimanglic species, form a dense, sediment-collecting basal mat; these rhizoids function in uptake of macronutrients from the substratum (Williams, 1984). *Caulerpa* species form wound-plugs when injured (Dawes and Goddard, 1978). Wound-plug response is a necessary adaptation in plants of coenocytic structure, in order to limit loss of cytoplasm when the outer membrane is disrupted. All shelled Ascoglossa (= Conchoidea of Gascoigne, 1985) are limited to this genus (Kay, 1968), and several Caribbean elysiids feed primarily on *Caulerpa*, but very few caliphyllids or stiligerids eat *Caulerpa*. Some *Caulerpa* species appear to specialize somewhat in habitat, while others are more generalized. For example, *C. cupressoides* (Vahl) C. Agardh and *C. lanuginosa* J. Agardh occur almost exclusively on coral-sand substrata, while *C. racemosa* and *C. sertularioides* occur on a variety of sediments, mangrove roots, and on rock substrata, and occur from mangrove areas to coral reef. The more restricted species are perhaps adapted to specific nutrient regimes.

A second group of species, represented by *Cladophora, Chaetomorpha, Bryopsis,* and *Cladophoropsis,* occurs loosely associated with a variety of substrata, ranging from drift algae to mangrove roots and occasionally on rock or sediments. These algae are typically filamentous, uniseriate and septate (except the coenocytic *Bryopsis*), are highly seasonal in occurrence (Croley and Dawes, 1970) and have low to medium ash content, from 16% (Clark, unpub.) to 40% (Jensen, 1983). Growth of these algae is apparently associated with high concentrations of dissolved nutrients (often predominantly vernal), which are extracted directly from the water column (since there is seldom direct contact of the algae with sediments). These algae are colonized almost solely by ascoglossans of stiligerid morphology (*Placida, Ercolania,* and *Hermaea*). Ascoglossan recruitment on these algae occurs primarily during cooler temperatures (less than 25°C) in tropical to temperate environments, and their ascoglossan populations are thus seasonal and frequently irruptive (Clark, 1975).

The third functional group contains primarily non-*Caulerpa* siphonalean chlorophytes (*Halimeda, Penicillus, Udotea, Cymopolia, Avrainvillea*). These algae are pseudoperennial, have moderate to heavy ash level (35-95%) (including an external layer of carbonate) and occur primarily in mesotrophic to oligotrophic habitats (e.g. coral-sand to coral reef). As in *Caulerpa*, basal rhizoids extend into sediment or adhere to rock surfaces (Hillis-Colinvaux, 1980) and are associated with uptake of nutrients from the sediment (Williams, 1984). These algae also form wound-plugs when damaged (our observ.). These algae are eaten by elysiids, caliphyllids, *Costasiella*, and boselliids.

There are, of course, forms transitional between these three major groups. The thallus in *Codium* is composed of a mass of uncalcified siphonaceous filaments (Prescott, 1968). This genus is eaten both by elysiids and stiligerids, and usually occurs in mesotrophic areas of high water flow (e.g. jetty communities).

Wound-plug formation in siphonalean algae probably increases feeding effort, and its absence in septate algae probably has an important effect on stiligeriform species' feeding rates. Jensen (1981) has noted buccal regurgitation in both septate and siphonalean feeding, but this process probably has different functions in the two types of algae. On septate algae, regurgitation can work against the rigidity of the cell wall, but in siphonalean algae, it could enzymatically counteract wound-plug formation.

Differences in ash level among externally calcified algae reflect the balance between organic growth and calcium carbonate deposition. High ash content can represent either relatively low growth rate (perhaps controlled by nutrient availability) or rapid skeletal deposition (as controlled by pH-temperature regimes). In reef environments, where high algal ash levels were observed, both influences operate, as dissolved nutrient standing stocks are low (Muscatine and Porter, 1977), while high photosynthetic rates in reef areas raise pH to levels that strongly favor carbonate precipitation. Intensive predation by reef herbivores (Lewis, 1985) can also favor high ash levels in reef algae. The mangrove habitats that we have examined have very few piscine herbivores, and mangrove areas generally have nutrient concentrations relatively high for tropical marine systems (Lugo and Snedaker, 1974).

In uncalcified algae, ash level more likely reflects the level of organic components of the cytoplasm: low-ash algae provide more nutrients for a given level of feeding effort. In either case, however, ash level provides a useful index of feeding effort.

Waugh and Clark (1986) found that feeding rates of *Elysia tuca* (as indicated by kleptoplastid uptake) were lower in animals that fed upon high-ash *Halimeda incrassata* than animals that ate low-ash *H. discoidea* Decaisne. Among the species of *Halimeda* we have examined, interutricular calcification also appears to negatively correlate with utricle diameter and degree of predation by elysiids. *Halimeda incrassata* and *H. discoidea*, for example, are relatively heavily grazed and have large utricles, while *H. monile* (Ellis and Solander) Lamouroux and *H. tuna* (Ellis and Solander) Lamouroux have small utricles and support very sparse ascoglossan populations (see Hillis-Colinvaux, 1980, Fig. 17, for relative dimensions of *Halimeda* utricles). *H. cuneata* has the lowest known ash content (33%) within the genus (Böhm, 1973). Though we have no data on predation on this species, Hillis-Colinvaux (1980, Fig. 36) illustrates a specimen of *H.*

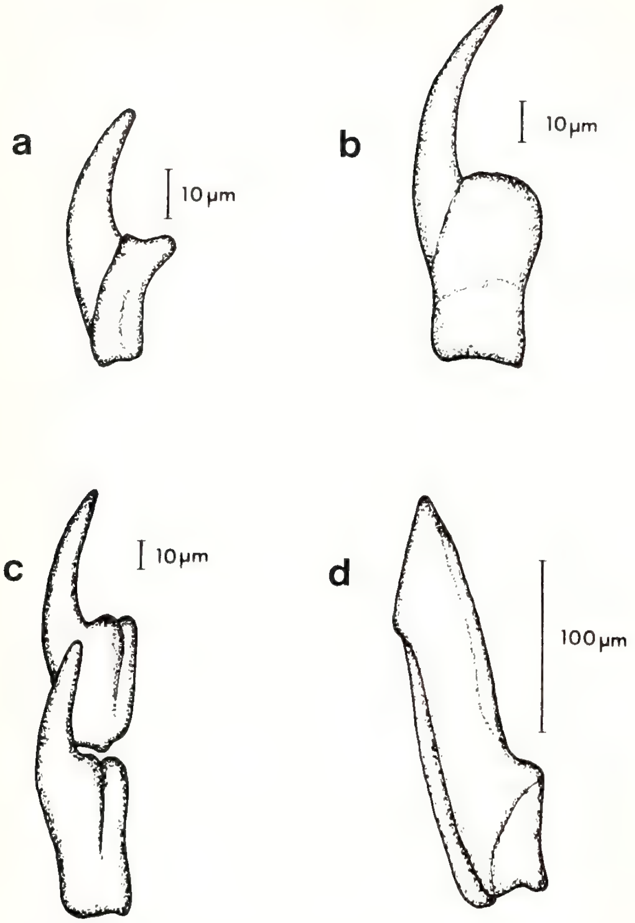


Fig. 23. Comparison of teeth of calciphilic species, showing *Halimeda*-spur (A, B, C) with caulerpivorous species (D) of *Elysia*. A = *E. papillosa;* B = *E. flava;* C = *E. tuca;* D = *E. subornata.* A, B, and E are from Clark, 1984; C is from Jensen and Clark, 1986.

cuneata with especially dense ascoglossan feeding tracks (probably of a *Bosellia*).

Caribbean elysiids that feed primarily on calcified algae (*Elysia tuca, E. flava* Verrill, *E. papillosa, E. patina* Marcus) often have a spurlike tip on the radular tooth (Fig. 23), while those that feed primarily on less-calcified algae [*E. subornata, E. ornata* (Swainson), *E.* sp. "AF"] have teeth with a broad tip. This "*Halimeda* spur" appears necessary to pierce the narrow utricles of *Halimeda* through the interutricular carbonate matrix.

The high densities noted for stiligerids, particularly in high latitudes, suggest that feeding effort is lower, and consequently growth and reproductive output are higher, for species feeding on septate, low-ash algae. Unfortunately, we have no data for high-latitude algal ash levels, but the biology of ascoglossans that eat high-ash foods suggest that feeding effort can constrain life history patterns. The transient, irruptive cycles of stiligerids (Clark, 1975) are probably unsupportable on algae of high ash content or siphonaceous structure because of lower feeding rates. Thus far, we have observed no examples of such cycles on siphonalean algae. Biomass ratios above 1% often lead to massive destruction of algal food resources in high latitude populations (Clark, 1975), but this overgrazing apparently does not occur on siphonalean algae.

Kleptoplastid retention is apparently absent among the Conchoidea, is relatively common among ascoglossans that feed upon high-ash algae (Elysiidae), and uncommon among those feeding upon low-ash algae (e.g. Stiligeridae). The energetic benefit of kleptoplastid maintenance would be greatest in species whose energy intake is limited by algal resistance to feeding. Indeed, noting the very low densities of reef populations, retention of kleptoplastids might be the only energetically feasible way that most ascoglossans can maintain populations in reef environments.

RELATIONSHIP OF ALGAL MORPHOLOGY AND PHYSIOLOGY TO ASCOGLOSSAN DIET:

Plastid morphology has been identified as one factor limiting the occurrence of kleptoplastids. Apparently, only "robust" plastids, generally spheroid in shape and usually occurring in coenocytic (siphonaceous) algae (Hinde and Smith, 1974), are able to survive ingestion and phagocytosis by ascoglossans. Plastids of septate algae (*Chaetomorpha, Cladophora*) used as ascoglossan foods are in contrast parietal, netlike, or fragmented in shape (Prescott, 1968), fragile, and break during ingestion. The functional basis for the robust nature of siphonalean plastids has not been defined. Their shape and size, however, are convergent with those of erythrocytes among a range of animal species, and we suggest that the shape and robustness of such plastids represent necessary adaptations to shear forces resulting from fluid transport in the cytoplasm of coenocytic algae, or, alternatively, that cytoplasmic streaming creates a less-controlled, less predictable intracellular environment that requires resistant plastid membranes.

Cytoplasmic streaming movements occur in Siphonales (Dawes and Barilotti, 1969), and the observed rapid uptake and transport of sedimentary nutrients by such algae (Williams, 1984) would seem to require large scale circulatory movements of cytoplasm (macrocyclosis). Further, this would explain the ecological dominance of siphonalean algae in oligotrophic environments, as sediments represent a nutrient sink and source of nutrient fixation unavailable to algae that lack rhizoidal uptake and coenocytic structure. Thus, the siphonalean algae often occupy a sediment-extractive niche similar to that of seagrasses, and several dominant siphonalean genera normally co-occur with seagrasses (Taylor, 1960). The xanthophyte genus *Vaucheria* is also sediment-associated, siphonaceous in structure, and supports kleptoplasty (Graves *et al.*, 1979).

The simpler, less-robust plastid membrane of non-siphonalean chlorophytes could also represent adaptation to higher external nutrient levels, in that membrane simplification would facilitate exchange of nutrients and permit higher plastid metabolic rates in situations where nutrient availability is relatively non-limiting (high latitude, eutrophic or mesotrophic habitats during vernal nutrient peaks).

The growth strategy of siphonalean algae involves a

Table 2. Ascoglossan population data. (Notes: * = mean of 2 or more samples; †secondary derivation (see text); (a) Warmke and Almadovar, 1972; (b) Brandley, 1j984; (c) Jensen, 1975. Habitats: FPJt = Fort Pierce Jetty; TCEm = Twin Cays Epimangle; LPPR = La Parguera reef, Puerto Rico; LSMF = Lake Surprise Mangrove; Channel Floor; CBC-RC = Carrie Bow Cay Reef Crest; SRBR = Sombrero Reef Crest, FL; TC-MP = Twin Cays Mangrove Pond; GKF = Geiger Key Coral-sand; SpHr = Spanish Harbor Coral-sand; NCT = Noank, CT; PCF = Pineda Cswy, Indian River Lagoon; HD = Hellebaek, Denmark; GKBp = Geiger Key Borrow-pit).

Species	Alga	Habitat	Lat'	Date	Temp. ^{0}C	Algal Dry Wt. (g)	Ash (%)	Biomass ratio	Density n/g dry wt
CONCHOIDEA									
Ascobulla ulla (Marcus and Marcus)	*Caulerpa racemosa*	FPJt	27.5	3 Apr 86	29	29.6		0.00443	0.574
Berthelinia caribbea Edmunds	*C. verticillata*	TCEm	17	9 Jun 85		1.49	28	0.0192	12.75
Lobiger souverbiei Fischer	*C. racemosa*	TCEm	17	7 Jun 85	29	55.2	58	0.00086	0.018
L. souverbiei	*C. racemosa*	FPJt	27.5	2 Jul 85	29	13		0.00181	0.077
Oxynoe antillarum Mörch	*C. racemosa*	TCEm	17	9 Jun 85		55.2	58	0.00053	0.0725
O. antillarium	*C. racemosa*	FPJt	27.5	2 Jul 85	29	13		0.00557	0.231
O. antillarum (a)†	*C. racemosa*	LPPR	18	Dec. 61		46.1			7.052
O. azuropunctata Jensen*	*C. paspaloides*	LSMF	25	27 Jun 85	27	17.9	24.5	0.00423	1.39
Volvatella bermudae Clark	*C. racemosa*	TCEm	17	9 Jun 85		55.2	58	0.00038	0.0181
BOSELLIIDAE									
Bosellia mimetica Trinchese	*Halimeda simulans*	CBC-RC	17	7 Jun 85		209	88	0.00015	0.0144
CALIPHYLLIDAE									
Cyerce antillensis Engel	*H. simulans*	CBC-RC	17	7 Jun 85		209	88	0.00016	0.0096
C. antillensis	*Penicillus dumetosus*	SpHr	24.5	25 Jan 86	23	26.8		0.00066	0.037
Mourgona germaineae Marcus Marcus*	*Cymopolia barbata*	GK	24.5	10 Sep 85	28	83.7	54	0.0005	0.13
ELYSIIDAE									
Elysia n. sp. "AF"*	*Caulerpa prolifera*	TVIR	29	12 Jun 86	27	15	14.9	0.0467	1.47
E. flava Verrill	*H. simulans*	CBC-RC	17	7 Jun 85		209	88		0.0096
E. furvacauda Burn (b)†	*Codium*	BBA	24.5	Oct 80		6.33			0.948
E. n. sp. "BL"	*H. simulans*	CBC-RC	17	7 Jun 85		209	88	0.00019	0.0239
E. papillosa Verrill	*P. dumetosus*	SpHr	24.5	25 Jan 86	23	26.8		0.00105	0.149
*E. papillosa**	*Udotea conglutinata*	SWC-RC	17	12 Jun 85		107	46.5	0.00078	0.122
E. sp. "ST"	*P. dumetosus*	SpHr	24.5	25 Jan 86	23	26.8		0.00159	0.037
E. subornata Verrill	*C. paspaloides*	LSMF	25	27 Jun 85	29	10.9	26	0.00171	0.551
E. subornata	*C. racemosa*	TCEm	17	9 Jun 85	29	15.3	62		0.719
E. tuca Marcus and Marcus	*H. simulans*	CBC-RC	17	7 Jun 85		209	88	0.00010	0.0239
E. tuca	*H. incrassata*	LSMF	25	17 May 86	26	35.1		0.00378	0.1425
E. tuca	*H. incrassata*	SRBR	24.5	26 Aug 86	29.5	94.9		0.00024	0.0211
COSTASIELLIDAE									
Costasiella ocellifera	*Avrainvillea nigricans*	TC-MP	17	16 Jun 85	30	8.6	49.5	0.0221	5.00
C. ocellifera	*A. nigricans*	GKF	24.5	10 Sep 85	29	5.1	36	0.0042	3.53
C. ocellifera	*A. nigricans*	LSMF	25	17 May 85	26	1.86		0.031	7.8
STILIGERIDAE									
Ercolania funerea (Costa)	*Cladophoropsis*	LSEm	25	5 Apr 86	29	5.65		0.00034	0.531
E. fuscata (Gould)	*Cladophora*	NCT	41	14 Jul 70	23	0.08		0.0103	723
E. fuscata	*Chaetomorpha*	NCT	41	10 Aug 70	23	1.51		0.00498	31.1
E. fuscata	*Cladophora*	PCF	28	6 Apr 86	27	1.48		0.0045	6.74
E. fuscata	*Bryopsis*	PCF	28	6 Apr 86	27	3.61		0.0033	5.82
Limapontia capitata (Mueller) (c)†	*Cladophora*	HD	56	18 Jun 75	17	1.85			40
Placida dendritica (Alder and Hancock)	*Codium*	NCT	41	20 Apr 70	18	3.89		0.0464	32.4
P. kingstoni (Thompson)	*Bryopsis*	GKBp	25	25 Jan 86	23	0.75		0.0447	24.2

strong component of vegetative propagation by stolonoid extension (Hillis-Colinvaux, 1980). This strategy presumably involves extensive reorganization and cytoplasmic transport, and might require mobilization of catabolic enzymes. Trench (1980) suggested that plastid "robustness" might represent resistance to (animal host) lysozymal hydrolases, but such resistance might originate in plastid resistance to intrinsic algal hydrolases. These enzymes could be unnecessary in the highly compartmentalized systems of septate algae of seasonal growth.

The effects of latitude on biomass ratio and population density could be partially due to ash levels, as calcium carbonate has an inverse thermal solubility and thus algal carbonate levels should decrease with latitude. However, other important latitudinal effects, including seasonality of nutrients and light, standing stock of dissolved nutrients,

Table 3. Possible coevolutionary adaptations of tropical algae and ascoglossans.

Algal adaptation	Possible ascoglossan response
secondary compounds	toxin tolerance; defensive sequestration; dietary selectivity
wound-plug response	buccal regurgitation, salivary enzymes
increasing ash level	radular modification; kleptoplasty
gamete satiation	facultative consumption of gametangia

levels of toxic secondary compounds, and thermal effects on metabolic rates, probably operate on ascoglossan populations.

Additional, unmeasured factors can also covary with ash content, and the effects of ash *per se* are probably exaggerated in the present study. Two effects, variation in level of toxic algal metabolites and variations in life history characteristics, probably affect our data.

POSSIBLE COEVOLUTIONARY ASPECTS OF ASCOGLOSSAN/ALGAL RELATIONSHIPS:

Toxic secondary algal metabolites are common in siphonalean algae (Norris and Fenical, 1982). Some of these are defensively sequestered by ascoglossans (Doty and Aguilar-Santos, 1970; Norris and Fenical, 1982; Jensen, 1984) and would appear non-toxic to these animals, but other toxins can inhibit recruitment, growth, and reproduction of ascoglossans. Higher levels of caulerpin and caulerpicin occur in algae preferred by Caribbean ascoglossans (Vest *et al.*, 1983), but whether this represents response by algae to predation or ascoglossan preference for higher toxin levels is undetermined. *Mourgona germainiae* appears to defensively utilize cymopols from *Cymopolia*; however, these are physically isolated from body tissues (Jensen, 1984), and are rapidly autotoxic to animals confined in small volumes of water. *Tridachia crispata* exhibits similar auto- and allotoxicity (pers. obs.). This suggests that even defensively sequestered compounds are potentially toxic, depending on concentration. Also, the elysiids that dominate Caribbean coral reefs (*T. crispata, Elysia subornata, E. tuca, E. papillosa*) feed upon a variety of siphonalean genera (Clark and Busacca, 1978; Jensen, 1980; present study) and are habitat generalists (Figs. 16, 17). This feeding strategy, in which feeding is dispersed over several plant species with varied metabolites, could maintain dietary intake of specific metabolites below toxic levels.

Janzen (1974) has noted that nutrient-poor terrestrial communities produce exceptionally high levels of defensive compounds in apparent response to herbivore selective pressure. Such an effect should also operate in marine systems, and the most obvious parallel is the coral reef.

A review of plant-herbivore coevolution in terrestrial systems (Rhoades, 1985) provides several interesting insect-plant interactions that can parallel ascoglossan-algal relationships. A summary of possible coevolutionary aspects of ascoglossan/algal biology is presented in Table 3. One possible parallel is the pattern of gametangia production in *Halimeda*. During this process, all tissue resources are suddenly channelled into gamete production, followed by death of the entire thallus (Hillis-Colinvaux, 1980). Gametangic thalli are strongly attractive to *Elysia tuca* (Waugh and Clark, 1986), and this reproductive mechanism apparently represents a predator-satiation strategy similar to mast-fruiting in some rain forest trees and bamboo (Janzen, 1974), necessary because gametangia are formed external to the calcareous framework of *Halimeda* thalli (Hillis-Colinvaux, 1980). Gametangia formation is synchronous in *H. incrassata*, the principle food of *E. tuca,* with about 25% of thalli in localized patches gametangious during rising spring temperatures at some localities (own obs.). Hillis-Colinvaux (1980) reports, however, that asynchronous formation of gametangia is normal among *Halimeda*.

OVERVIEW OF ASCOGLOSSAN EVOLUTION:

The maximum densities and diversity of tropical Caribbean ascoglossans occur in the transition between coral-sand and mangrove habitats. This habitat is heavily colonized by sediment-associated *Caulerpa* species. We suggest that the first ascoglossans evolved in this habitat as burrowing forms (Kay, 1968; Clark and Busacca, 1978). Other major radiations involved adaptation to utilize other functional algal types, with accompanying modification in life histories (Fig. 22).

Two major evolutionary thrusts are evident. At one extreme, ascoglossans have evolved to exploit high-ash algae as found in the coral-sand habitat and especially on the coral reef. Populations in these habitats are strongly limited by algal resistance to herbivory (especially by skeletal carbonates and latex) and exist at low densities. At the other extreme, ascoglossans have very successfully exploited septate aglae in predominantly mesotrophic habitats and occur in high-density, transient populations.

The first major adaptive radiation, from sediment-associated caulerpivores, led to non-burrowing shelled Ascoglossa feeding on epimanglic and epilithic *Caulerpa* species. Transitions from burrowing to epilithic *Caulerpa* habitats occur in *Ascobulla* (DeFreese, in press; this study) and *Volvatella* (Clark, 1982), while the Oxynoidae, Juliidae, and Lobigeridae are entirely non-burrowing and are predominantly, but not exclusively, epilithic or epimanglic. Other radiations involved exploitation of septate algae, seasonally common in epimanglic habitats, by stiligeriform species, followed by adaptation to higher latitudes, and exploitation of externally calcified siphonales by caliphyllids, boselliids, and particularly elysiids. These algae are well-represented in the coral-sand habitat, and apparently reef-dwelling, kleptoplastid-retentive, calciphilic forms represent the most advanced species in this radiation.

In inshore habitats, at least, ascoglossans are probably the most significant predators on calcified Siphonales, and might have had a significant effect on evolution of these algae. Fossil Juliidae, representing the second radiation described above, are known from the Eocene (Kay, 1968), proving an ancient relationship between ascoglossans and siphonalean algae (because all shelled Ascoglossa feed only on *Caulerpa*). However, Hillis-Colinvaux (1980) considers *Halimeda* an evolutionarily conservative genus, and fossil *Halimeda* predate known ascoglossan fossils, occurring at least from the Cretaceous and possibly Jurassic. Thus, it appears that calcification in this group preceded ascoglossan feeding and probably has not significantly increased in response to ascoglossan herbivory.

The intimacy and antiquity of the ascoglossan-chlorophyte relationship suggest that ascoglossans could have exerted important effects on the evolution of chlorophytes, selecting for increased levels of ash and secondary compounds. The low density of ascoglossans in West Atlantic reef systems, however, suggests that the current balance of ascoglossan-algal coevolution favors the algae, presumably forcing major adaptations in ascoglossan life histories, such as a predominance of direct development (Clark and Goetzfried, 1978; Clark and Jensen, 1981) and kleptoplasty. High latitude coastal regions represent an opposite trend, in that ascoglossans often have major seasonal impact on algal populations, commonly overgrazing the food supply to the point of destruction (Clark, 1975).

Important aspects of ascoglossan-algal interactions remain to be explored. Quantitation of algal metabolites, for example, might determine whether algae proximally respond to herbivory by increased toxin production, and would clarify latitudinal and habitat effects. Analysis of ash content in distinct clonal populations of algae might also help to explain patchiness of ascoglossan populations.

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DISTRIBUTION AND ECOLOGICAL ADAPTATIONS OF INTERSTITIAL MOLLUSCS IN FIJI

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ABSTRACT

Interstitial molluscs in the Fiji Islands were found in coarse sands associated with coral reefs and beaches. Characteristically the sand was moist, lacked any sulfides and was in an area of constant water exchange. Representative taxa found included species in the class Aplacophora and in the opisthobranch orders Nudibranchia, Philinoglossa and Acochlidiacea. Of these groups, the acochlidiaceans were most numerous in genera represented; the acochlidiacean, *Paraganitus ellynnae* Challis, was the most common species while all others were found in small numbers.

A model for evolution of the marine and freshwater acochlidiaceans in island habitats is presented based on adaptation of interstitial ancestors.

Interstitial molluscs inhabit pore spaces in high-energy, coarse-sand environments. They have been recorded from intertidal and subtidal habitats in both tropical and temperate waters and show remarkable adaptations for their specialized environment (Swedmark, 1968a). Representatives are found in the Aplacophora (subclass Neomeniomorpha) and in the Gastropoda (subclass Opisthobranchia: orders Acochlidiacea, Philinoglossacea and Nudibranchia).

Interstitial solenogasters (Aplacophora) have been described (Marian and Kowalevsky, 1886; Salvini-Plawen, 1968, 1985; Morse, 1979) but up to the present time have not been recorded from South Pacific Islands. Salvini-Plawen (1985), in his description of three new species, referred all solenogasters modified for an interstitial habitat to the family, Meiomeniidae. Acochlidiacean opisthobranchs often are the major component of the molluscan interstitial fauna in coarse sand habitats. These organisms are known from detailed species descriptions, e.g. Bergh (1895), Kowalevsky (1901), Odhner (1937a, b, 1952), Marcus (1953), Marcus and Marcus (1954, 1955) and Swedmark (1968b). Challis (1968, 1970) recorded three species from the South Pacific, *Paraganitis ellynnae* Challis from the Solomon Islands and the new Hebrides and *Pseudunela cornuta* (Challis) and *Maraunibina verrucosa* (Challis) from the Solomon Islands.

Other opisthobranchs adapted for an interstitial environment include interstitial nudibranchs, referred to the genus, *Pseudovermis.* This genus has a worldwide distribution and frequently co-occurs (although in fewer numbers) with the acochlidiaceans. Two species have been described from the South Pacific, *P. mortoni* Challis from the Solomon Islands and *P. hancocki* Challis from New Zealand (Challis, 1969a). The interstitial Philinoglossacea are also represented by one genus, *Philinoglossa* which is found less frequently. However, Challis (1969b) described *P. marcusi*, from the Solomon Islands.

A survey of coarse sand habitats on Viti Levu and adjacent islands in Fiji was conducted in 1978-79 to locate interstitial molluscs. A more systematic study was undertaken at Korolevu beach when it was found to be the richest collecting site. This beach is also the type locality for an interstitial priapulid, *Meiopriapulus fijiensis* Morse (Morse, 1981). Based on the distribution of acochlidiaceans at Korolevu, a hypothesis is proposed for the evolution of interstitial and freshwater acochlidiaceans.

METHODS

Collections were made at localities (Fig. 1) accessible by car and/or boat around the main island of Viti Levu. A transect from high tide to low tide on the beach at Korolevu indicated that interstitial molluscs occurred at approximately the same tide levels in substrata of similar quality and partical size as I had previously observed in other parts of the world. Subsequent areas of sampling were based on this observation. At all localities, sand samples were taken from coarse sand around reefs or from coarse sand beaches that were well-oxygenated, without visible sulfides present in the

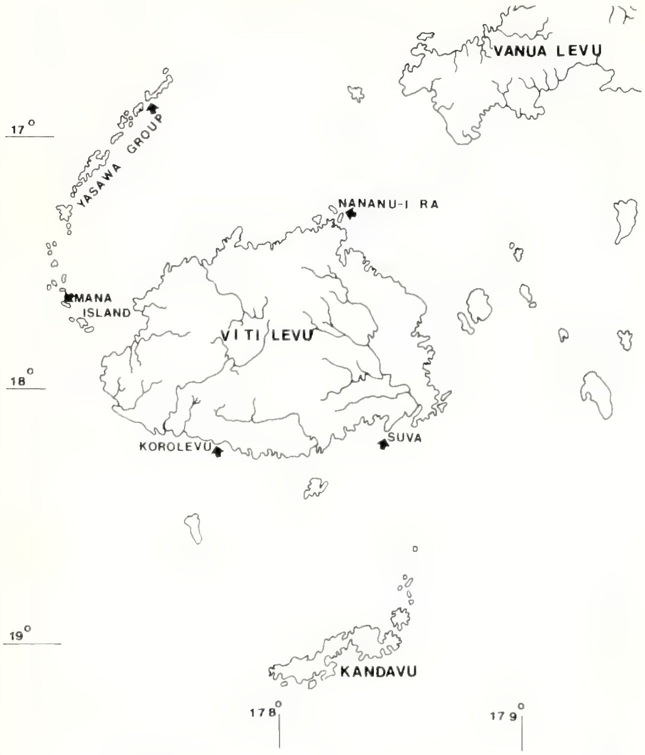

Fig. 1. Map of the Fiji Islands with collecting areas where interstitial molluscs were collected designated by arrows.

sands or fluctuating salinities. Whenever one species of interstitial mollusc was found and if the schedule allowed, more samples were taken from that locality. Cores of sand approximately 10 cm high and 5 cm wide were collected with a garden trowel and individually placed in plastic bags. Subtidal samples were collected in about 1 m of water near the edge of Suva Reef. All samples were transported back to the laboratory of the Institute of Marine Resources at the University of the South Pacific in Suva where living organisms were extracted by elutriation, photographed, studied and fixed in 70% alcohol or Hollande's fixative. Although numerous areas were sampled at any one locality, only those where interstitial molluscs were found are reported.

DESCRIPTION OF COLLECTING SITES

Suva reef is a fringing reef at the outer portion of the delta of the Rewa River. Interstitial molluscs were found there in two habitats. One site was a series of small pockets just inside the algal ridge. These holes were about 0.5 m in depth and often strewn with calcareous sand; they harbored holothurians that break down the chunks of coral into smaller particles. Coarse sand was often banked on the most protected side of the hole. Fine sediments were absent. Water in the holes is continuously exchanged by surge at low tide and the entire area is covered at high tide. The other habitat for interstitial molluscs was along the edge of the channel through the reef. In this passage the surge from wave action is continual and the coarser sand is located along the channel edge. Extensive sampling in the great expanses of sand substratum behind the reef did not yield any interstitial molluscs. This habitat may be unsuitable owing to freshwater intrusion during severe rains. On one occasion, 20 cm of rain was recorded in 24 hr and mud suspended in freshwater runoff from the Rewa River was seen to extend all along the shore side of the reef.

Interstitial molluscs were found in sand from three islands near Viti Levu: Nananu-i-ra off the northeast coast, and Mana Island and the Yasawa Group off the northwest coast. At Nananu-i-ra, coarse sand samples collected from around the bases of dock pilings yielded interstitial molluscs. At all sites the sand was taken from low intertidal regions near the fringing reefs or from subtidal habitats.

Numerous samples were collected at Korolevu, a resort area on the mid-south shore of Viti Levu where a fringing coral reef is located very close to the shoreline (Fig. 2). First suggested as a likely place for interstitial fauna by Professor John Ryland (pers. comm.), the beach is located landward of an inlet in the fringing reef, with a relatively deep offshore channel leading up to the beach. An intermittent stream flows into the inlet from the surrounding hills. Although protected, the area is continually washed by waves and is therefore considered as a high-energy beach.

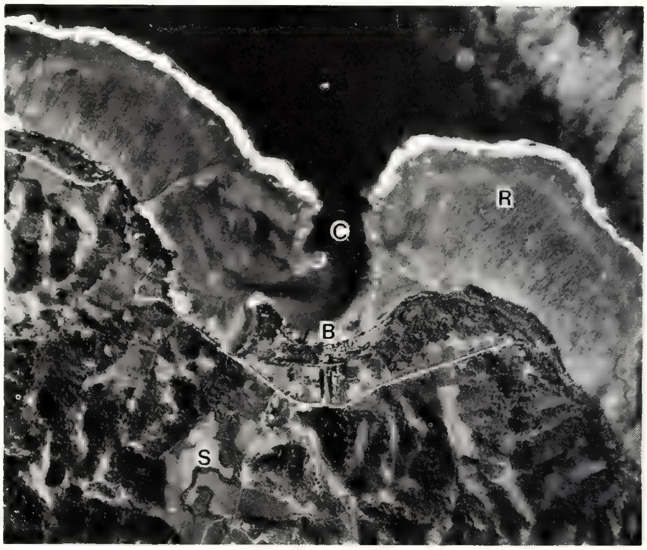

Fig. 2. Photograph of Korolevu showing the beach where interstitial mollluscs were collected. Note the freshwater stream (S), the deep-water channel (C), the fringing reef (R) and the beach (B). The line represents the position of the transect on the beach.

The most systematic collection of interstitial molluscs was made at Korolevu Beach along a transect established 50 m east of the resort building and extending 15 m from the low tide mark up the beach toward a group of palm trees (Figs. 2, 3). The average slope of the beach was 7°. The sand was a mixture of clastic and coral components with an average phi number of 0.25 and standard deviation of 1.48. There was a sargassum bed just subtidal to the transect. Samples were

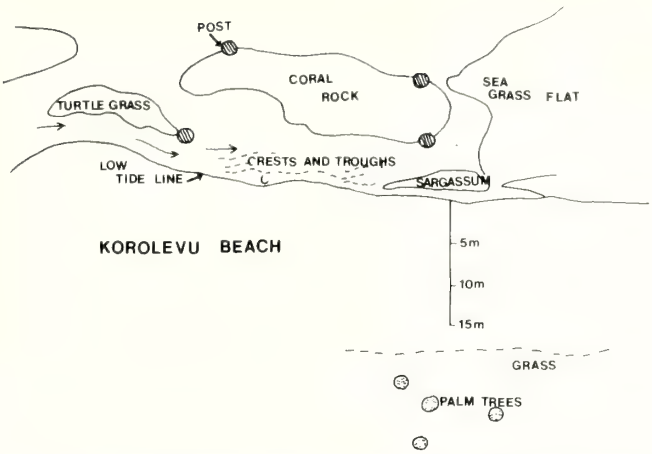

Fig. 3. Diagram of the study area at Korolevu Beach. Cross-hatched circles represent wooden posts and dotted circles represent palm trees.

taken at 1, 2, 3 and 5 m from the low tide line (0.3 m tide) after removal of the dry surface sand. Each sample measured approximately 400-500 cc. Above 5 m, the sand was very dry. Additional samples were taken from a subtidal crest and trough region caused by local currents in an areas to the left of the transect.

SPECIES OF INTERSTITIAL MOLLUSCS COLLECTED

Eight species of meiofaunal Mollusca were found in this study; they are listed in Table 1 and illustrated in figure 4. All except one are Opisthobranchia, with four species in the Acochlidiacea, one in the Philinoglossacea and two in the Nudibranchia. In addition, one species of Aplacophora (subclass Neomeniomorpha) was found at Suva Reef. With the exception of *Paraganitus ellynnae*, the interstitial molluscs were found in small numbers at all habitats examined.

At Korolevu interstitial molluscs were most numerous near the low tide mark at 1 and 2 m (samples I and II, Table 2). These samples were dominated by *Caecum* sp., a minute prosobranch gastropod that feeds on algae. This species also dominated the adjacent subtidal crest and trough region. The acochlidiacean, *Paraganitus ellynnae*, was the most numerous of the four species collected along the transect and the only mollusc found at 5 m. As the sand became dry higher on the beach, samples were taken at increasingly deeper levels. At 5 m from low tide, the wet layer was 12 cm deep; there was a dramatic decrease in numbers of interstitial mollluscs with only a single specimen collected.

In the subtidal crest and trough zone, interstitial molluscs were well represented. Comparing the two areas, the crests were dominated by *Caecum* and more species and individual interstitial molluscs were found in the troughs between the crests. Again, the dominant species was *Paraganitus ellynnae.*

The other opisthobranchs collected at Korolevu included a less common species of acochlidiacean, *Pseudunela* sp., *Pseudovermis* spp. (eyeless and eyed) and *Philinoglossa* sp. Associated interstitial taxa were *Meiopriapulus fijiensis, Saccocirrus* sp., *Protodrilus* sp., *Polygordius* sp., nematodes, turbellarians and copepods.

Table 1. Interstitial molluscs from Viti Levu, Fiji.

Classification	Locality Collected
Class Aplacophora)	
Subclass Neomeniomorpha	
Meiomenia sp.	Suva Reef
Class Gastropoda	
Subclass Opisthobranchia	
Order Acochlidiacea	
Paraganitus ellynnae	Korolevu; Yasawa Island
Pseudunela sp.	Korolevu; Yasawa Island
Hedylopsis sp.	Suva Reef; Yasawa Island
Gastrohedyle sp.	Suva Reef; Nananu-i-ra
Order Philinoglossacea	
Philinoglossa sp.	Korolevu; Mana Island
Order Nudibranchia	
Pseudovermis sp. (eyeless)	Korolevu
P. sp. (eyed)	Korolevu; Suva Reef

Among the island collections, the sand beaches of the Yasawa Group had the greatest diversity with three species of acochlidiaceans (Table 2). More systematic collections are needed in these islands.

DISCUSSION

In Fiji, the dominant group of interstitial molluscs are the acochlidiaceans. Their abundance and position on the beach are similar to those reported by Challis (1969c, d) on the Solomon Islands, but the only species similar in Fiji to those found by Challis was *Paraganitus ellynnae*. This acochlidiacean was also the most abundant species at Korolevu.

In common with the occurrence of interstitial molluscs in other localities (Morse, 1976, 1979), the species collected in Fiji were always associated with sand in areas of continual water exchange and in the absence of sulfides. The sand can be well sorted as was found in the reef pockets on Suva reef or with a mixture of sized particles as shown by the standard deviation from the average phi size from the Korolevu Beach sample.

Distribution of interstitial molluscan genera appears to be cosmopolitan. The occurrence of well known genera in Fiji substantiates this idea. In the Fijian habitats, the acochlidiaceans were of particular interest. They are the only opisthobranchs that are known to have evolved freshwater species and six of the approximately 30 known species of acochlidiaceans are described from freshwater island habitats. In the South Pacific, several species have been found in mountain streams in Indonesia (Bergh, 1895; Bucking, 1933), the Island of Palau (Bayer and Fehlmann, 1960), and the Solomon Islands (Wawra, 1974).

These freshwater species differ from marine species

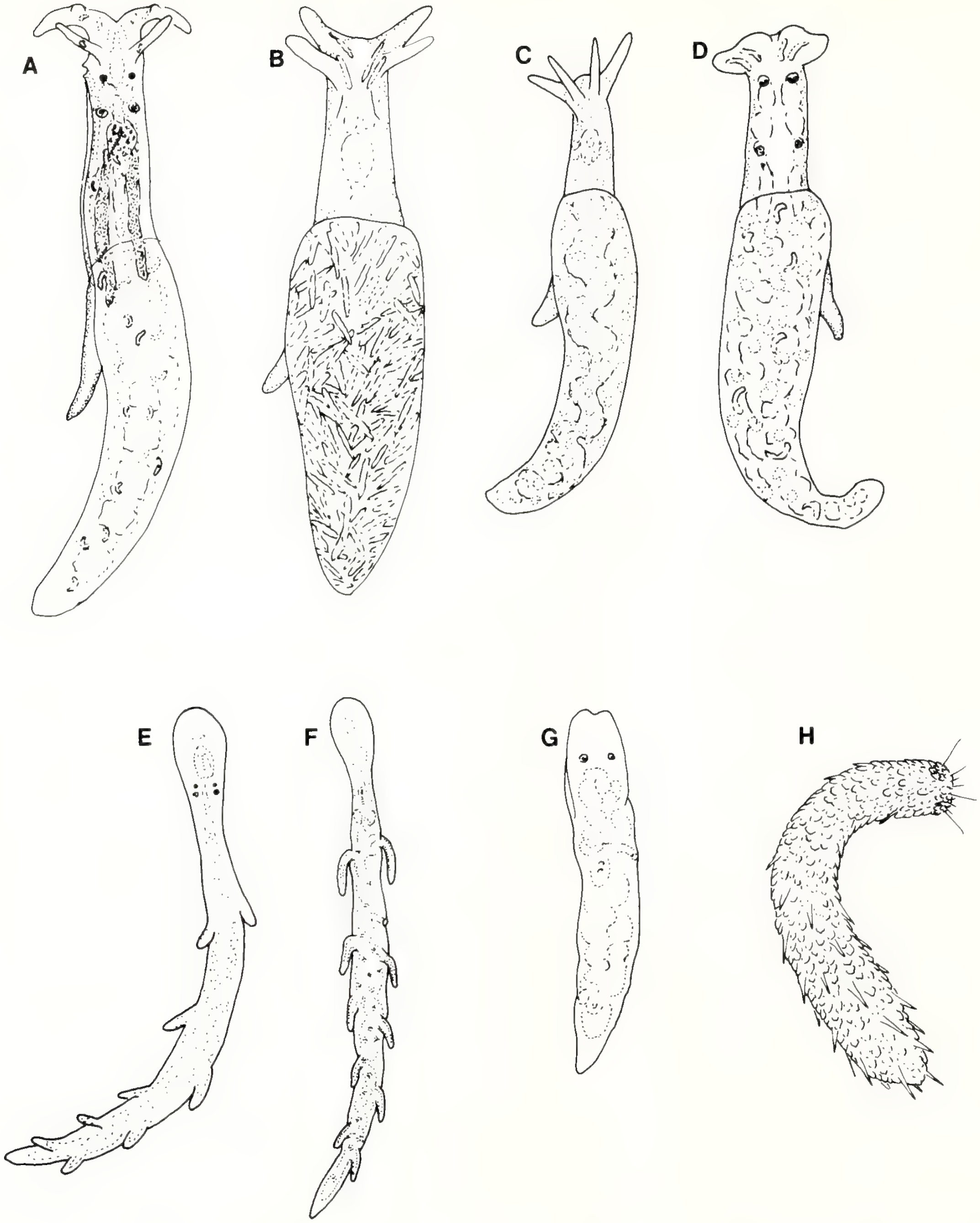

Fig. 4. Drawings of the interstitial molluscs from coarse sand environments on Viti Levu, Fiji: **A.** *Pseudunela* sp. (3.5 mm long); **B.** *Hedylopsis* sp. (1.2 mm long); **C.** *Paraganitus ellynnae* (2.5 mm long); **D.** *Gastrohedyle* sp. (1.2 mm long); **E.** *Pseudovermis* sp. (eyed, 4 mm long); **F.** *Pseudovermis* sp. (eyeless, 3.5 mm long); **G.** *Philinoglossa* sp. (2.3 mm long); **H.** *Meiomenia* sp. (1.3 mm long).

in habitat and size. They live in mountain streams on the underside of rocks and range in size from 3 to 8 mm in length. Those that have been described have a well developed heart-kidney complex and accessory male reproductive structures such as a penis and penis stylet. Professor Starmuhlner (University of Vienna) collected freshwater forms from the undersides of rocks in Fiji (pers. comm.). In my collections in Fiji, four genera of marine interstitial acochlidaceans were found. If the freshwater forms were derived from the interstitial acochlidiaceans, it would be predicted that the ancestral group would have internal structures, that is, accessory reproductive organs and kidney, that were similar. One of the species collected, *Pseudunela* sp., was found to have a well developed heart, a large kidney and a penis with a stylet. Thus

Table 2. Species of interstitial molluscs collected on intertidal transect and subtidal crest and trough zone at Korolevu Beach.

Intertidal - on transect from algal region at edge of low tide to 5 meters.

	Paraganitus ellynnae	*Philinoglossa* sp.	*Pseudovermis* sp.	*Pseudunela* sp.	Environment
Sample I (1 meter)	39	1	0	1	rock and sand, not well-sorted, dominated by *Caecum*
Sample II (2 meters)	74	0	3 (eyeless)	0	well-sorted coarse sand, wet layer 2 cm deep, abundant *Caecum*
Sample III (3 meters)	9	0	1 (eyeless)	0	well-sorted coarse sand, wet layer 5 cm deep
Sample IV (5 meters)	1	0	0	0	well-sorted coarse sand, wet layer 12 cm deep, very dry above

Subtidal - crest and trough zone

	Paraganitus ellynnae	*Philinoglossa* sp.	*Pseudovermis* sp.	*Pseudunela* sp.	Environment
Sample V (crest)	8	1	1 (eyed)	0	coarse shell sand, dominated by *Caecum*
Sample VI (trough)	19	1	1 (eyeless)	1	coarse shell sand, coral chunks

it could be a relic of the stem group that evolved both the stream forms and the other interstitial genera. The other marine interstitial species (*Hedylopsis, Paraganitus,* and *Gastrohedyle*) found in the Fijian sands show regressive evolution toward a vermiform body, a type of evolution first described by Swedmark (1968a). They have a reduced cell number resulting in a simplified reproductive system, a single digestive gland and a reduced or lost heart-kidney system. It would be further predicted that a relic group would be associated with the shores of these islands from which freshwater species have been described. Indeed, Challis (1970) found and described another *Pseudunela, P. coronuta* (Challis), from the Solomon Islands. To test this prediction, more species of marine interstitial acochlidiaceans from island habitats where freshwater species are known should be investigated to see if there are ancestor-like genera present in the interstitial sands.

Climatic conditions that, over time, could have had an impact on such patterns of evolution were witnessed during my tenure in Fiji. They included a hurricane, "Melibe", that changed the topography of Korolevu beach, and floods due to 20 cm of rainfall in 24 hours that impacted the areas behind Suva reef. Freshwater runoffs have created breaks in the fringing reefs, such as is seen at Korolevu, resulting in landward sandy beaches where interstitial molluscs are found. Hurricanes and floods could have been responsible for extensive reassortment of the beach sediments and unsteadiness of habitats that led to further speciation of the acochlidiaceans.

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Dr. Eveline Marcus for whom this symposium is dedicated, encouraged me early in my work on opisthobranch molluscs to be sure to study the "inside of organisms". In 1974, she facilitated an expedition to Brazil, opening to me her collecting sites, scientific expertise, and her home as I struggled to find new interstitial molluscs.

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AEOLID NUDIBRANCHS AS PREDATORS AND PREY

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ABSTRACT

The biology and autecology of aeolid nudibranchs are much better known than are the roles nudibranchs play in the communities in which they occur. This report describes known and potential roles aeolid nudibranchs play as both predators on cnidarians and other taxa and as prey to higher trophic level predators.

Aeolid nudibranchs are well-known predators of sessile cnidarians, particularly hydroids, anemones and corals (Hyman, 1967). There is an extensive literature on the systematics (i.e. McDonald, 1986), biology and ecology of aeolids (Swennen, 1961; Miller, 1961, 1962; Thompson, 1964; Thompson and Brown, 1984; Harris, 1973; Clark, 1975; Nybakken, 1974, 1978; Todd, 1981, 1983). The two recent reviews by Todd (1981, 1983) summarize much of what is known about the ecology and reproductive biology of nudibranchs. This information relates primarily to the autecology of the group, particularly locality and seasonality data and information on food preferences. Few studies have focused on the potential roles of aeolid nudibranchs within the communities in which they exist. This is equally true of their roles as both predators and as prey. The information that is available suggests aeolid nudibranchs can play significant parts in communities occupying hard substratum. The purpose of this report is to describe aspects of aeolid ecology that indicate their possible impact on the communities in which they occur and to speculate on the mechanisms by which they influence community development and organization. The emphasis will be first on nudibranchs as predators and then as prey.

AEOLIDS AS PREDATORS

Most aeolid nudibranchs are partial predators consuming portions of colonial prey such as hydroids, octocorallian and scleractinian corals (Todd, 1981). Even many anemone-eating species feed on anemones that form aggregations or clones or are too large as individuals to consume in a single meal. This mode of predation has several implications for prey species populations: (1) physical gaps in the colony, aggregation or clone can be formed; (2) the population structure of the prey can be altered; and (3) the prey can respond by growth and/or behavioral changes. Any such change is likely to alter interspecies interactions and hence community structure.

PREDATION ON OPPORTUNISTS

Hydroids are often one of the first groups of organisms to colonize disturbed or newly available surfaces (Harris and Irons, 1982). Many hydroids appear to follow the general pattern described for opportunists in community succession by Connell and Slatyer (1977); they may dominate space for a period, but they seldom replace themselves because succeeding generations fail to appear and they ultimately give way to later successional stage species.

The presence of hydroids can influence the sequence or species composition in the successional sequence. Standing (1976) found that colonies of *Obelia* inhibited the recruitment of barnacles because the polyps ate the cyprids and stolons interferred with settlement, while tadpole larvae of the tunicate *Mogula* were able to recruit successfully. The next stage of succession was altered from a barnacle-dominated system to one occupied by tunicates. Russ (1980) showed that tufts of string simulating hydroids facilitated the successful establishment of tunicates and bryozoans by protecting the young stages from fish predation. Dean and Hurd (1980) found that hydroids increased the recruitment of mussels onto fouling panels. In most cases, hydroids are described as being early colonists and being replaced without any information on why they do not persist or whether they can influence the succeeding stages of the community.

One reason why hydroids are unlikely to persist is the recruitment of aeolid and dendronotid nudibranch predators that ultimately consume the hydroids (Orton, 1914; Lagardere and Tardy, 1980; Harris and Irons, 1982). Even in algal-dominated communities, hydroids and nudibranchs may be one of the earliest ephemeral stages in community development. Within six weeks of a February, 1983 storm that caused high sea urchin mortality, facilitating the reestablishment of kelp beds in many communities along the coast of Southern California (Ebeling *et al.*, 1985; Harris *et al.*, 1984), many of the scoured surfaces at Naples Reef in the Santa Barbara Channel were covered with stolon networks of thecate hydroids. These hydroids were heavily infested with small aeolids including *Eubranchus* spp., *Cuthona albocrusta* (MacFarland), and *Hermissenda crassicornis* (Eschscholtz) (Harris, unpublished observations).

Nudibranchs in low densities are unlikely to seriously damage a hydroid colony since colonial forms grow at exponential rates while the individual nudibranch will feed at an arithmetic rate. Evidence from one study suggests that nudibranch predation may induce changes in hydroid growth form. Gaulin *et al.* (1986) showed that predation by the nudibranch *Tenellia adspersa* (Nordmann) caused an increased stolon budding rate in the hydroid *Cordylophora lacustris* Allman. The critical factor in inducing this change in growth form was a factor associated with *T. adspersa* mucous, because forceps and nudibranch mucous caused increased stolon budding while removal of polyps by forceps alone inhibited stolon budding completely. Nudibranch predation should result in a denser colony growth form in *Cordylophora.* Folino (1985) found indications of altered growth form in colonies of *Hydractinia echinata* (Fleming) in response to feeding by *Cuthona nana* (Alder and Hancock). If this phenomenon of altered growth from cropping nudibranch predation is widespread, it could influence the effectiveness of hydroid colonies as larval filters (Standing, 1976) and add a stochastic influence to subsequent community development. The induction of spines for defense by predator substances is already well-documented in other groups such as rotifers (Gilbert, 1980) and bryozoans (Harvell, 1984). Cropping by ungulates has been shown to stimulate certain grasses to form denser stands by vegetative growth (McNaughton, 1984; Belsky, 1986).

High densities of nudibranchs can result in the total destruction of a hydroid colony. The buildup of nudibranchs on a hydroid population is also likely to have a secondary impact, the inhibition of subsequent hydroid recruitment. New colonies of hydroids are unlikely to survive where a high density of nudibranchs is encountering a decreasing food source. The perisarcs of the initial colonies will remain after the polyps have been consumed much as the effect of defoliation of trees by herbivores. As with the remaining herbivores, the resident nudibranchs will inhibit the recruitment of new hydroid colonies of the same species. Clark and Clark (1984) reviewed the literature pertaining to the models proposed by Janzen (1970) and Connell (1971) to explain high tree species diversity in tropical rain forests. The model states that seeds and seedlings of rain forest trees will suffer highest mortality near adults of the same species due to an accumulation of herbivores associated with that species. Clark and Clark (1984) found that the literature relating to the Janzen-Connell Model was mixed, though generally supportive. While the mechanisms determining tropical rain forest tree species diversity are likely to be several and complex, the patterns of hydroid-nudibranch turnover suggest that the Janzen-Connell Model may be at least one mechanism explaining why hydroids generally do not replace themselves in early successional stage communities. Observations of algal dominated communities in the Gulf of Maine suggest that small herbivores such as the prosobranch *Lacuna vincta* (Montagu) may have a similar impact on early successional stage algae such as *Ulva* spp. and filamentous rhodophyta (Lubchenco, 1986; Harris, in press).

Hydroids with their arborescent growth forms and exoskeletal perisarc enhance topographic relief on new surfaces. The skeleton elevates the colony into the water column for feeding, but it also provides physical structure for setting nudibranchs and the larvae of later successional stage organisms such as mussels and tunicates (Standing, 1976; Harris and Irons, 1982; Dean and Hurd, 1980). The physical structure of opportunists may provide refuges from predators, both on micrograzers such as nudibranchs and the young stages of competitive dominants (Russ, 1980). It may be that opportunists such as hydroids and filamentous algae are their own worst enemies, because the physical structure provides settling surface and protection from predation for both their predators and competitors.

PREDATION ON LONG-LIVED SPECIES

Some cnidarians, such as sea anemones and corals, are long-lived and capable of assuming the role of competitive dominant in certain communities. Cloning sea anemones such as *Anthopleura elegantissima* (Brandt) and *Metridium senile* L. can dominate considerable space in intertidal and fouling communities respectively (Sebens, 1979; Hoffman, 1976; Harris and Irons, 1982). The aeolid nudibranch *Aeolidia papillosa* (L.) is a major predator on anemones in northern Atlantic and Pacific coastal environments. Schick *et al.* (1979) proposed that the population structure of *M. senile* at a site on the Maine coast was due to predation by *A. papillosa.* Studies by Harris on the West Coast (1976) and East Coast (1986) of the United States have shown that *A. papillosa* is a size-selective predator on *M. senile* due to the effectiveness of acontia extrusion as a defense by large anemones. Laboratory and field studies have shown that nudibranch predation is at least one mechanism that can account for some populations of *M. senile* being dominated by solitary and small aggregations of large individuals, while in areas of low nudibranch numbers, *M. senile* occurs in large clones dominated by small specimens (Harris, 1986).

A number of studies described chemotactic behavior in *Aeolidia papillosa* (Stehouwer, 1952; Braams and Geelen, 1953; Harris and Duffy, 1980; Hall *et al.*, 1982, 1984) and prey preference among a range of anemone species (Waters, 1973; Edmunds *et al.*, 1974, 1976; Harris and Howe, 1979; Hall *et al.*, 1982, 1984; Hall and Todd, 1986; Harris and Duffy, 1980; Harris, 1986). Ingestive conditioning (Wood, 1968) has been demonstrated by Hall *et al.* (1982) and Harris and Duffy (1980), but Hall *et al.* (1984) were not able to conclusively show switching behavior (Murdoch, 1969). A conflict over whether *Metridium senile* is a preferred prey of *A. papillosa* has been evident in the literature for some time with most prey-selection experiments tending to suggest that *A. papillosa* does not prefer *M. senile* (Waters, 1973; Edmunds *et al.,* 1974, 1976; Harris and Howe, 1979; Hall *et al.,* 1982, 1984; Hall and Todd, 1986). However, *A. papillosa* is found associated with *M. senile* in both the Pacific and Atlantic Oceans (Harris, 1973, 1976, 1986) and does show a preference for *M. senile* in olfactometer tests when fed small individuals of the anemone (Harris and Duffy, 1980). The apparent conflict seems to be due to the fact that most investigators use larger sized individuals of *M. senile* which have an effective defense in acontia extrusion that is most effective under laboratory conditions (Harris, 1986).

Nudibranch predation on anemones makes space available on hard substrata both by consumption of anemones and by escape responses such as crawling (Edmunds *et al.,* 1976; Harris and Howe, 1979), swimming (Robson, 1966; Harris, 1973) or releasing from the substratum (Rosin, 1971; Harris, 1973; Edmunds *et al.,* 1976). Cloning anemones such as *Metridium senile* are effective space occupiers and may be competitive dominants in fouling communities or on undercut surfaces in the rocky subtidal (Harris and Irons, 1982; Harris, 1986). The disturbance caused by nudibranch predation opens space for other species to recruit, thereby potentially increasing diversity in these communities. Anemone-eating nudibranchs can, therefore, serve a similar function in fouling communities to that of *Pisaster* in the rocky intertidal, a keystone predator (Paine, 1966). It may be stretching the point to claim that aeolid nudibranchs are keystone predators, but some species are capable of preventing space monopolization by certain anemones. *Coryphella salmonacea* (Couthony) in the Gulf of Maine (Morse, 1971) and *Hermissenda crassicornis* in California (Harris, personal observation) feed on colonial tunicates that can become major space occupiers. However, the most likely nudibranchs to have a major impact on the climax communities of many fouling and cryptic communities are the large sponge-eating dorids so prevalent in some regions, since sponges have the potential to be very effective long-term space competitors (Harris and Irons, 1982; see Wells *et al.,* 1964).

AEOLID NUDIBRANCHS AS PREY

There has been much speculation about predation on nudibranchs, presumably because there are a number of large, brightly colored species that wander about in the open without being attacked. A number of authors have offered nudibranchs to fish with the result that the nudibranch is grabbed, mouthed and rejected (Harris, 1973; Todd, 1981). In his detailed study of aeolid nudibranch secretory glands and cnidosacs, Edmunds (1966) concluded that predation by visual hunters must have been a strong evolutionary selective pressure.

Several predators of nudibranchs have been identified. Paine (1963) conducted extensive prey preference studies on the cephalospidean *Navanax inermis* (Cooper) and showed that it will eat many species of nudibranchs including aeolids.

The notaspidean *Pleurobranchaea californica* (Dall) will eat a number of aeolid and other nudibranchs (Harris, unpublished observations). In the Pacific Northwest, the seastar *Crossaster papposus* (L.) readily feeds on nudibranchs (Mauzey *et al.,* 1968), but eats seastars in the Atlantic (Hancock, 1955; Hulbert, 1980). Various crabs and lobsters have been cited as potential predators, but there is little evidence (Harris, 1973; Todd, 1981). Fish predation has received the most attention, presumably due to the conspicuous coloration of many nudibranchs and the fact that fish are visual predators.

Todd (1981) reported that wrasses ate small aeolids and saccoglossans exposed when coral heads were overturned in the Red Sea. Harris (1973) proposed that fish predation must be important as a selective force based on studies of two species of aeolids in the coral-eating genus *Phestilla.* Both species are cryptic in coloration and behavior, deriving their coloration from coral pigments and/or zooxanthellae. Neither species of *Phestilla* stores nematocysts from their coral prey, apparently because coral nematocysts are no protection against the numerous fish species that actively feed on corals. The cnidosacs in *Phestilla* spp. have become secretory glands (Harris, 1973). Harris (1986) reported on fish predation on the dorid *Onchidoris bilamellata* (Alder and Hancock) and the aeolid *Aeolidia papillosa.* Both species were found in the stomach contents of large (> 30 cm) specimens of the winter flounder *Pseudopleuronectes americanus* (Walbaum).

Harris (1986) also conducted field and laboratory studies of predation by the wrasse *Tautogolabrus adspersus* (Walbaum) on the aeolid *Aeolidia papillosa.* The results showed that *T. adspersus* does eat *A. papillosa,* but that the relative sizes of predator and prey are important, with the fish taking smaller size classes. Since *A. papillosa* is seldom common, most of the fish predation must be both size-selective and investigative in nature. *A. papillosa* is least common among *Metridium* populations where fish are aggregated such as caves, breakwaters and pilings, and more common in open habitats where fish are uncommon (Harris, 1986). It appears that the presence of wrasses has a negative impact on *Aeolidia* recruitment to those sites where fish are common and this allows the development of large aggregations of small-sized *Metridium.* In contrast, the absence of fish allows a buildup of *Aeolidia:* being a size-selective predator on *Metridium,* this could result in scattered populations of anemones dominated by large individuals.

COLORATION AND MIMICRY

Aeolidia papillosa is brownish in color with some populations having a white mottling. Individuals are nocturnal and tend to hide or remain in a contracted state during the day. The larger contracted individuals closely resemble a sea anemone with their many cerata looking like tentacles. It is clear that *Aeolidia* is cryptic in form, coloration and behavior. At the opposite extreme are species such as *Hermissenda crassicornis* of the West Coast of the United States which are large, strikingly colored and conspicuously active by day. The question of whether an aeolid is cryptic or aposematic must include the size, habitat and behavior of the species, as well as the possession of a noxious defense.

It is most likely that all aeolids less than 10 mm are cryptic due to their size and the heterogeneous nature of the background represented by most assemblages of benthic organisms (see Edmunds, 1974). This would be similar to a skunk that is cryptic at a distance in the mosaic of shadows and moonlight in a temperate woodland at night when skunks are active. Even the striking patterns of many small aeolid species blend with the background and these species are seldom found away from their hydroid prey. For those species that do grow beyond 10 to 15 mm, most appear to remain cryptic due to a combination of coloration and nocturnal or inconspicuous behavior. Over half of the aeolid species known from the Gulf of Maine are crytic due to size, coloration and behavior as adults (Harris, unpublished observations) while at least 25 of the 35 species of aeolids reported from the West Coast by Behrens (1980) and McDonald and Nybakken (1980) are apparently cryptic.

Species that are aposematic in coloration and behavior such as *Coryphella verrucosa* (Sars) in the Gulf of Maine and *Hermissenda crassicornis* are distasteful to fish and avoided. Wrasses that readily fed on *Aeolidia papillosa* would not touch *C. verrucosa* (Harris, 1986). Efforts to induce feeding of wrasses and surfperch on *Hermissenda* at Naples Reef in the Santa Barbara Channel were fruitless, even though numerous smashed sea urchins were placed among the nudibranchs, the fish actively selected the pieces of urchin without touching the nudibranchs. In a similar test the same species of fish consumed individuals of the cryptic *Dendronotus frondosus* (Ascanius), *Hancockia californica* MacFarland and *Elysia* sp. with minimal stimuli from broken urchins (Harris, Lambert and Laur, unpublished observations).

If warning coloration does occur in some aeolid nudibranchs, then it is possible that mimicry could occur in some groups (Wickler, 1968; Edmunds, 1974). Of the two major forms of mimicry, Batesian and Müllerian, the latter seems more likely since many species have arrays of secretory glands that appear to be defensive in function (Edmunds, 1966; Harris, 1973; Todd, 1981) and almost all aeolids store nematocysts. One possible example of Batesian mimicry could involve the aeolid *Hermissenda crassicornis* (which does apparently have warning coloration) and the arminid *Antiopella barbarensis* (Cooper). *Antiopella* has a similar morphology and coloration, though it eats bryozoans and does not store nematocysts. It could be that *Antiopella* and *Hermissenda* are equally distasteful, but no work has been done on this species. The author has observed numerous co-occurring specimens of these two species in the intertidal at Dillon Beach, California. The cerata of both species were yellowish in color and it required careful inspection to tell them apart.

Rudman (1982, 1983) has documented the regional occurrence of species complexes of tropical dorids from several genera. Each grouping of species has a distinct color pattern making identification of live specimens difficult. Most of the species are in the genus *Chromodoris*, all of which tend to have large marginal secretory glands that are presumably defensive in nature. This appears to be an example of Müllerian mimicry similar to the complexes of distasteful butterflies described from the tropics (Wickler, 1968; Edmunds, 1974). Goddard (1987) suggested that the dorids *Crimora coneja* Marcus, *Laila cockerelli* MacFarland and *Triopha catalinae* (Cooper) from the coast of California could form a mimicry complex, but was unsure whether it would be Mullerian or Batesian.

A possible example of Müllerian mimicry in aeolid nudibranchs exists in the Gulf of Maine on the east coast of the United States. In the region, there is a low diversity of epibenthic feeding fish (Bigelow and Schroeder, 1953), with the wrasse *Tautogolabrus adspersus* being the most obvious. There is also a low diversity of known nudibranch species (Harris, 1973; Gosner, 1971) with the present known number being 32. There are 13 species of aeolids that have a broadly similar color pattern of reddish ceratal digestive diverticula with white tips [*Cuthona concinna* (Alder and Hancock), *C. nana, Catriona gymnota* (Couthony), *Eubranchus tricolor* Forbes, *E. sanjuanensis* Roller, *Facelina bostoniensis* Couthony, *Setoaeolis pilata* (Gould), *Coryphella verrucosa, C. verrilli* Kuzirian, *C. salmonacea, C. nobilis* Verrill, *C. gracilis* (Alder and Hancock), *C. pellucida* (Alder and Hancock)]. This species complex comprises 40% of the nudibranch fauna in the southern Gulf of Maine. The wrasse *T. adspersus* rejects *C. verrucosa* which is one of the most common large aeolids in the region and this nudibranch may serve as the model. It could be that the low diversity of visual predators in this region has led to one conspicuous color pattern being selected for. Mimicry in nudibranchs could be far more common than realized and nudibranchs could prove to be excellent models for the study of visual predation as a selective force on the evolution of marine invertebrates.

CONCLUSIONS

The biology and autecology of aeolid nudibranchs has become increasingly well documented (see McDonald, 1986), but little is known about the roles played in marine benthic communities by this common group of molluscs. Aeolids are among the most common predators on cnidarians which are conspicuous occupiers of primary space in the successional sequences of many hard substratum communities and we know little about the contributions of either predator or prey. The processes in which they are participating are often dynamic and take place at rates faster than the sampling periodicities of most ecological studies. The advantage of this fast turnover time is the possibility of conducting short-term experiments that have the potential of providing insights into the mechanisms that determine the patterns observed over longer time scales.

Hermissenda crassicornis and *Aeolidia papillosa* provide just two examples of species that have interesting possibilities for ecological study. *Hermissenda* beings life as a micrograzer on ephemeral hydroids such as *Obelia* (Harrigan and Alkon, 1978). It is cryptic and is one of a suite of species that ultilmately overwhelms the established colonies and could prevent recruitment of more colonies of the same species. *Hermissenda* grows to greater than 40 mm in length and assumes the role of predator not only on hydroids, but also on small hydroid-eating aeolids as well as colonial tunicates that are space competitors in later successional stage fouling communities. *Hermissenda* is diurnal and aposematic in coloration and behavior; it could also serve as a model for mimicry from at least one nudibranch species that is not even an aeolid. *Aeolidia papillosa* is a specialist on sea anemones at all stages of its benthic existence. It is cryptic in coloration, behavior and probably morphology with its prey anemones serving as models. *Aeolidia* could play a role not unlike a keystone predator by opening space in anemone aggregations and, therefore, preventing space monopolization by species that are capable of being effective space competitors.

This review of information relating to the roles of aeolid nudibranchs in marine benthic communities is designed to stimulate discussion and suggest gaps in our knowledge that require our attention rather than to provide definitive answers. It is hoped that more detailed study of aeolid nudibranchs as both predators and prey will not only add to our knowledge of the group, but will help us to understand the processes by which marine benthic communities function.

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REPRODUCTIVE ENERGETICS AND LARVAL STRATEGIES OF NUDIBRANCH MOLLUSCS: EFFECTS OF RATION LEVEL DURING THE SPAWNING PERIOD IN *ONCHIDORIS MURICATA* (MÜLLER) AND *ADALARIA PROXIMA* (ALDER AND HANCOCK)

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ABSTRACT

The nudibranchs *Onchidoris muricata* (Müller) and *Adalaria proxima* (Alder and Hancock) prey preferentially upon the same species of bryozoan, have annual life cycles, semelparous life history strategies and reproduce at much the same time of year. They differ, however, in body size and larval type; the larger *(A. proxima)* reproduces by short-term pelagic lecithotrophic larvae while the smaller *(O. muricata)* has long-term planktotrophic larvae. *O. muricata* allocates absolutely less, but relatively more, energy to reproduction and shows a tight allometric relationship between body size and fecundity. For *A. proxima,* variation in body size explains only ≃ 25% of the variance in individual fecundity, with larger adults producing fewer offspring on a weight for weight basis. Maximization of fitness in *O. muricata* depends, to a large extent, on continued feeding and diversion of assimilated products to current reproduction. *A. proxima* adults appear less able to exploit such recurrent energy, and the suggestion is that this underlies selection for lecithotrophy. (The higher individual larval probabilities of successful metamorphosis conferred by short-term pelagic lecithotropic veligers are presumed to damp the variance in individual fecundity.) This was further evaluated by subjecting both species to differing ration levels (= energy availability) during the reproductive period. The two species responded similarly (on a proportional basis) to ration level, in respect to a range of independently appraised reproductive criteria, but a major contrast was noted for a composite measure of individual daily reproductive 'performance'. *A. proxima* was largely unaffected by ration level, whereas *O. muricata* displayed marked and significant decreases in fecundity, especially on starvation. The implications of the individuals' energetics in explaining selection for particular larval strategies in nudibranch species are discussed.

Three features have become axiomatic within the ecological study of reproductive strategies. First, individual adults will produce as many offspring as possible. Second, individual energy budgets are finite and there are, in consequence, limits to what is possible. Third, there are "costs" associated with expenditure within each component of the budget and, for this reason, we might expect offspring production to be 'optimised', rather than maximised. Within the general framework of life history theory the concept of reproductive "effort" (that is, the proportion of total budget resources diverted to reproductive function) has become a central construct (e.g. Fisher, 1930; Williams, 1966; Tinkle, 1969; Gadgil and Bossert, 1970; Pianka, 1970, 1976; Schaffer, 1974; Stearns, 1976). The energetic costs incurred in reproduction might be most simply envisaged as a reduction in future reproductive potential arising from the diversion of resources away from maintenance, at the expense of possible continued adult survivorship. This principle necessarily extends to consideration of the circumstances which affect and dictate the two fundamental demographic features of the individuals' overall life history strategy; that is, the duration of the adult phase (subannual, annual, biennial or perennial life-cycle strategies) and the frequency of reproductive events [i.e. semelparous (single) or iteroparous (repeated) strategies]. Benthic marine molluscs are perhaps of especial interest to these broader issues, by virtue of their not only displaying the entire spectrum of life-cycle and life history strategies, but also in possessing a variety of pelagic (free-swimming) or non-pelagic larval forms.

Planktotrophic larvae hatch from small eggs, are 'poorly-developed' and require extended periods feeding and growing in the plankton prior to settlement and benthic metamorphosis (Thorson, 1946). Lecithotrophic larvae hatch from intermediate/large eggs and can be briefly pelagic (but usually non-feeding) or wholly non-pelagic. Thorson (1946) estimated that 80% of benthic marine invertebrates reproduce by means of planktotrophic larvae. This particular feature is, therefore, of some considerable interest, particularly because there are reasons to suppose that planktotrophy is the 'primitive' or 'ancestral' state in a wide variety of phyla (including Mollusca), and, moreover, that the lecithotrophic category is a largely irreversible evolutionary derivative (Strathmann, 1978). What remain to be resolved, therefore, are the selective factors that have dictated such putative evolutionary shifts to the more advanced larval types.

Our investigations have concentrated upon nudibranch molluscs (e.g. Todd, 1979a, b; Todd and Doyle, 1981; Todd and Havenhand, 1983; Hall and Todd, 1986; Havenhand *et al.*, 1986). The rationale of our approach is that energetic considerations outline the bounds of possibility, and that some form of optimisation of individuals' reproductive allocation underlies selection for particular larval types. It is, perhaps, important to emphasize that selection does not necessarily demand efficiency (in terms of numbers of offspring per joule of reproductive allocation): selection ought to favour that strategy which confers the largest number of surviving offspring, even if (perhaps by a particular larval strategy) these are apparently produced "inefficiently" (Todd, 1985). Moreover, functional energetics are not the only parameter in the equation: the differing larval types presumably confer markedly different genetic consequences, especially in terms of individual larval survivorship to metamorphosis, and dispersal potential.

The present paper comprises an extension of previous analyses of reproductive allocation in two species of dorid nudibranchs, *Adalaria proxima* (Alder and Hancock) and *Onchidoris muricata* (Müller) (Todd, 1979a; Todd and Havenhand, 1983). These species are ecologically comparable in occupying similar niches, preying preferentially upon the same species of bryozoan [*Electra pilosa* (L.)], having the same (annual) life-cycle and life history (semelparous) strategies, and reproducing at much the same time of year. Both are simultaneous hermaphrodites and lay their eggs in gelatinous benthic spawn masses. They differ, however, in their egg sizes and individual fecundity (85 μm, 6-50 x 10^3, *Onchidoris*; 170 μm, 2-40 x 10^2, *Adalaria*) and larval type: *Onchidoris* has long-term planktotrophic larvae (Todd and Havenhand, 1985), while *Adalaria* has briefly pelagic lecithotrophic veligers. *Adalaria* larvae can feed, but do not require to do so in completing development and metamorphosis; the larvae are pelagic for perhaps a minimum of 1-2 days and will only metamorphose on contact with the live bryozoan prey (Thompson, 1958). *Onchidoris,* on the other hand, undergoes an extended pelagic phase metamorphosing after perhaps 35 days in the plankton (Todd and Havenhand, 1985). The contrasts in egg size and larval type thus confer markedly different egg to benthic juvenile periods, at the same temperature, and contrasting larval transport potential.

Previous analyses of these species showed two striking features. First, the lecithotrophic strategy correlated with an absolutely higher (but relatively lower) level of caloric investment, and second, there is a highly significant allometric relationship between body size and fecundity in *Onchidoris murciata* but only a marginally significant relationship for *Adalaria proxima* (Todd, 1979a; Todd and Havenhand, 1983). For the analysis of spawn calories (y) on body calories (x) the regression coefficients, r^2, n, and significance levels were: *O. muricata,* 1.83, 0.64, 15, $P < 0.001$; *A. proxima,* 0.34, 0.25, 19, $P < 0.05$. Thus, larger individuals of *Adalaria* generally produce fewer offspring on a weight-for-weight basis than do smaller conspecifics. Indeed, for *Adalaria* only 25% of the variance in individual fecundity is explained by variation in body size, by contrast to 65% for *Onchidoris.*

There are reasons to suggest that these two species share a recent common evolutionary ancestry (Havenhand *et al.*, 1986) and that *Adalaria* is the more advanced derivative. The question to be resolved, therefore, is why *Adalaria* should have been selected for lecithotrophy. It was previously suggested (Todd, 1979a) that this relinquishing of planktotrophy could concern an adaptive response to the above mentioned unpredictability of energy diversion to reproduction in *Adalaria* adults; the lecithotrophic strategy is presumed to confer the higher probability of individual larval survival to metamorphosis. In consequence lecithotrophy might comprise the 'safer' mode of reproduction by decreasing individual variance in reproductive success.

MATERIALS AND METHODS

The primary objective of this study was to analyse the effects of differing levels of energy availability ("ration level") during the reproductive period on: (1) measurable fitness components (e.g. spawn mass sizes and numbers, total reproductive allocation); (2) survivorship; and (3) copulatory activity for isolated pairs of these molluscs. This approach is ecologically valid in view of the decidedly patchy distribution of the prey bryozoan. Three ration levels were adopted. The first grouping concerned "fully-fed" control pairs, in which nudibranchs were fed *ad libitum* in a manner consistent with that prior to the onset of spawning for all pairs. The second was a "half-ration" grouping, in which pairs, immediately following first spawning, were provided with *Electra* for a period of days, starved for a similar period, and re-fed/starved for a differing period, and so on. All pairs for both species at half-ration encountered the same sequence of availability/unavailability of *Electra* following their first spawning. Periods were selected from random digit tables with the objective of providing the nudibranchs with unpredictable access to *Electra* which, over the (then unknown) duration of the spawning period, would result overall in an $\simeq$50% availability. The third was a "starved" grouping in which molluscs were denied *Electra* throughout, following first reproduction for each pair. The data concern, for *Adalaria*

15, 10 and 8 pairs, and for *Onchidoris* 13, 10 and 12 pairs in the "fully-fed", "half-ration" and "starved" treatments respectively.

Pairs of nudibranchs were maintained throughout in small mesh cages placed in the one aquarium, through which fresh seawater (at ambient field temperatures) flowed continuously to waste. Food was provided as *Electra* colonies epiphytic on *Fucus serratus* (L.). Cages were inspected daily with observations of copulatory activity being made and, where appropriate, spawn masses removed and food changed. When *Electra* was added the nudibranchs were placed on the bryozoan itself and, if copulating, care was taken to not separate the pair during transfer.

Spawn masses were examined for fertility and if cleavage had not commenced the diameters of ten zygotes were measured to the nearest micrometre. Every spawn mass was then mounted between glass slides and a silhouette projected using a photographic enlarger. This permitted the error-free enumeration of all eggs. Egg totals for all spawn masses were converted to dry weights, and thence caloric (joule) equivalents using previously derived predictive regressions (Todd, 1979a). Individual nudibranchs were regularly damp-weighed to provide body sizes of reproducing adults and, again, these converted to their joule equivalents (Todd, 1979a). Body sizes were invariably maximal at the commencement of reproduction. Reproductive effort was quantified as the turnover ratio [Total spawn joules ÷ maximum post-spawning body joules (for the pair) x 100] used previously (Todd, 1979a; Todd and Havenhand, 1983; see Hall and Todd, 1986 for further discussion). For logistic reasons it was impracticable to monitor a sufficient number of replicates of both species at either ration level in any one year. Accordingly, data for each ration level were collated in 1979, 1981 and 1982, with the fully-fed (control) pairs being supplemented by observations from a previous study (Todd, 1979a). Locations of the field sources for both species are given in Todd and Havenhand (1983).

Because the variation in most of the parameters considered below was non-normal both inter- and intra-specific comparisons were undertaken non-parametrically using Mann-Whitney U-tests. For convenience the data for the respective species are graphically presented as 'reproductive responses': that is, the half-ration and starved treatments expressed as a proportion of the respective control groupings. (The outcomes of the U-tests are not altered by such standardization.) Throughout the analyses median (not mean) values were utilised and these are plotted together with their respective upper and lower quartiles, as indicative of variances.

Among the criteria evaluated for each pair in the respective groupings, total spawnings and egg total are self-explanatory, but the remainder require qualification: Number of copulations — Copulation was first observed usually some days prior to first spawning, and continued throughout the spawning period. The present analyses concern only those copulations following first spawning; Copulation days — This is a truncated measure of reproductive longevity, in being the number of days from first spawning to first death; Days between copulations — This was determined by dividing copulation days by number of copulations for each pair; Spawning days — This is the sum of the two periods from first spawning to first and second deaths for each pair and is, therefore, a measure of reproductive longevity; Days between spawnings — This is similar to days between copulations; Egg total, minus first spawnings — Because the half-ration and starved treatments were initiated only following first spawning, the more appropriate evaluation of fecundity, spawn size, and reproductive effort is with the first spawn masses excluded; Daily reproductive allocation in relation to ration taken — While the analyses of the above characteristics in isolation should prove informative, this study focuses on the overall day-to-day "performance" of the reproducing adults adjusted for body size and longevity. The rationale is that although senescence and death are innately determined, extrinsic mortality agents may act at any time. "Ration taken" is a composite of the ration available (1.0, 0.5 or 0) scaled downwards in making allowance for copulatory activity during periods of *Electra* provision; feeding does not, apparently, continue during coupling (pers. obs.). Because nudibranchs were inspected only once daily it has been assumed for present purposes that copulating pairs did not feed on that day (if food was actually available at half-ration), and that pairs not copulating would have fed whenever *Electra* was provided. Clearly, the latter may not pertain but any bias (for the control and half-ration pairs) should be similar throughout. Although variable both within- and between-species, the rate of egg production towards the end of the spawning period generally decreases somewhat (Todd, 1979a, Todd and Havenhand, unpubl. obs.); for convenience these allocations were assumed to remain constant and hence are simply expressed as spawn J·body $J^{-1}\cdot day^{-1}$.

RESULTS

No significant differences (U-tests) were found for body sizes between treatments for *Onchidoris,* but a marginally significant ($p = 0.042$) difference was observed between the control and starved pairs for *Adalaria*; here, the median joule equivalents for fully-fed and starved pairs were 668J and 396J respectively. Within- and between-group differences in body sizes within species should not, however, markedly affect the analyses.

The outcomes of the intra- and inter-specific comparisons for the data presented in figures 1 and 2 are summarized in Tables 1 and 2, respectively. The between-treatment tests for the two species (Table 1) apply equally to the untransformed and control-standardized data. The comparisons in Table 2 are, however, based upon the standardized values: in essence, these tests evaluate whether or not the two species differed (at half-ration or starved) in their proportional responses scaled to the median value observed for their respective control groupings. Attention should also be drawn to the frequently high variances observed for the rather small sample sizes.

NUMBER OF COPULATIONS (Fig. 1a)

Copulation of some pairs was frequently scored for up

Table 1. Outcomes of U-tests between treatments for both species for the variables considered in the text and illustrated in Figures 1 and 2 (see text for details). Where significant differences were observed the ration grouping showing the greater value is also indicated (* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$; ns = not significant).

	Fully-fed vs. Half-ration (1.0 vs. 0.5)		Half-ration vs. Starved (0.5 vs. 0)		Fully-fed vs. Starved (1.0 vs. 0)	
	Adalaria proxima	*Onchidoris muricata*	*Adalaria promixa*	*Onchidoris muricata*	*Adalaria proxima*	*Onchidoris muricata*
Number of copulations	**FF<HR	ns	ns	**HR>S	ns	ns
"Copulation days"	ns	ns	ns	ns	ns	ns
Days between copulation	*FF<HR	ns	ns	**HR<S	ns	**FF>S
Total spawnings	ns	ns	ns	**HR>S	*FF>S	***FF>S
"Spawning days"	ns	ns	ns	ns	ns	**FF>S
Days between spawnings	ns	ns	ns	**HR<S	ns	*FF<S
Egg total	ns	ns	**HR>S	**HR>S	**FF>S	***FF>S
Egg total, minus first spawnings	ns	ns	*HR>S	**HR>S	**FF>S	***FF>S
Spawn size, minus first spawnings	ns	*FF>HR	*HR>S	**HR>S	**FF>S	***FF>S
Reproductive effort, minus first spawnings	ns	ns	*HR>S	*HR>S	**FF>S	***FF>S

Table 2. Inter-specific outcomes of U-tests for both the "half-ration" and "starved" treatments (standarised on their respective species' "control" groupings) in terms of the variables compared intra-specifically in Table 1. (*A.p.* = *Adalaria proxima; O.m.* = *Onchidoris muricata;* * = $P<0.05$; ** = $P<0.01$; ns = not significant).

	Half-ration	Starved
Number of copulations	**A.p.* > *O.m.*	ns
"Copulation days"	**A.p.* > *O.m.*	ns
Days between copulations	ns	ns
Total spawnings	ns	ns
"Spawning days"	***A.p.* > *O.m.*	ns
Days between spawnings	ns	ns
Egg total	ns	***A.p.* > *O.m.*
Egg total, minus first spawnings	ns	ns
Spawn size, minus first spawnings	ns	ns
Reproductive Effort, minus first spawnings	ns	ns

to six consecutive days. For analytical purposes each daily observation was considered a separate event although it would not be possible to distinguish these from a single protracted coupling.

DAYS BETWEEN COPULATIONS (Fig. 1c)

For both species there were overall trends of decreases in the intervals between copulations. Whether this is attributable to an increase in frequency or duration of copulation cannot be ascertained but the net effect is that at reduced ration the nudibranchs engage in this non-energy-acquiring activity to a greater extent. In view of the importance of continued feeding to reproductive allocation this is, therefore, a possible cost to fitness.

EGG TOTAL, MINUS FIRST SPAWNINGS (Fig. 2h)

The outcome for this criterion remains almost unchanged (with respect to g.) although the significant inter-specific difference (Table 2) is lost.

SPAWN SIZE, MINUS FIRST SPAWNINGS (Fig. 2i)

Figure 3 illustrates the frequency distributions of spawn mass sizes within each treatment for both species and distinguishes the first spawn masses from those subsequently laid. Strikingly similar patterns of response to ration level were noted for both species. The summed first two spawn masses produced by each pair did not differ significantly between treatments for either species (P ranging from 0.135 to 0.644), but the size and absolute number of subsequent spawnings declined very significantly ($P<0.001$). Egg sizes did not differ significantly between the treatments for *Onchidoris* but *Adalaria* showed a more variable pattern (Table 3). Nevertheless, the possibility remains that energy density per egg declines with ration: this could have incurred slight over-estimates of spawn caloric equivalents at reduced ration.

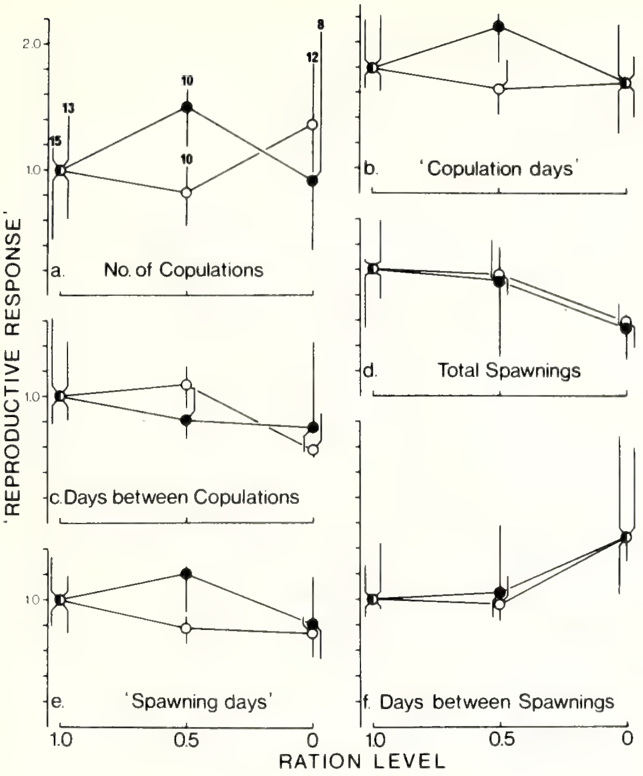

Fig. 1. Responses of *Adalaria proxima* (infilled circles) and *Onchidoris muricata* (open circles) to the half-ration (0.5) and starved (0) treatments, expressed as a proportion of their fully-fed (1.0) controls. Values are medians, with upper and lower quartiles also indicated. The number of replicate pairs for each species are given in figure 1a.

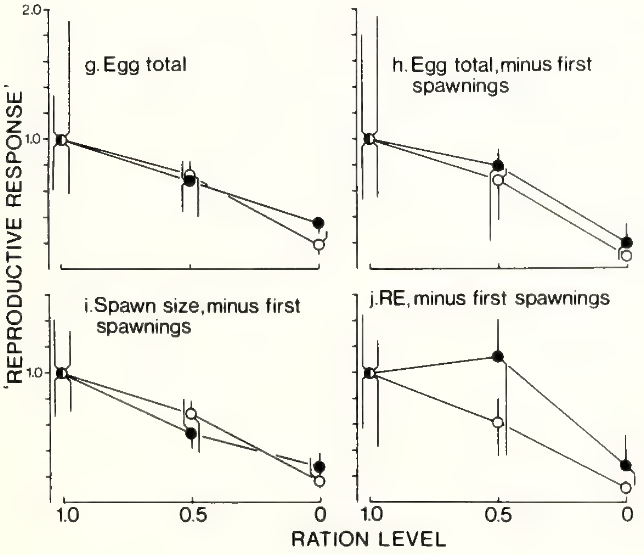

Fig. 2. Further reproductive responses of *Adalaria proxima* and *Onchidoris muricata* to the dietary treatments, as in figure 1. (RE = Reproductive Effort).

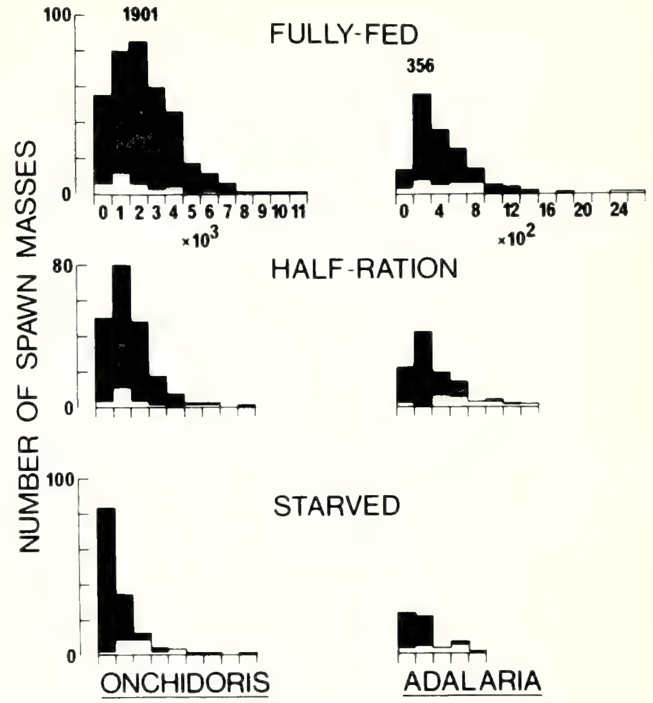

Fig. 3. Histograms of spawn mass sizes for all groupings of both species. Values on the abscissa show the number of eggs per spawn mass and in all cases are mid-points of the size-classes. The unshaded components in the histograms indicate the summed first two spawn masses for pairs in each grouping. Median sizes of spawn masses in the control groupings are also given for each species.

REPRODUCTIVE EFFORT (RE), MINUS FIRST SPAWNINGS (Fig. 2j)

The variances in these data are particularly large. However, in view of the poor relationships between body sizes and fecundity (see Introduction), the especially high variance for *A. proxima* at half-ration is unsurprising. These data provide further evidence of the inadequacy of simple turnover ratios in expressing individual reproductive "effort".

DAILY REPRODUCTIVE ALLOCATION, IN RELATION TO RATION TAKEN (Fig. 4)

As outlined above, the most appropriate analysis concerns the data with the first spawnings deleted. For comparative purposes figure 4 includes plots both "inclusive" and "exclusive" of these spawnings. For *Adalaria* no significant differences between treatments were noted for the inclusive data; for the exclusive plot there were no significant differences between adjacent groupings, but there was a significant ($P < 0.05$) decrease in daily allocation for starved versus control pairs. For *Onchidoris* there was no significant difference between the fully-fed control and half-ration pairs, but a marked and significant ($P < 0.001$) decrease in allocation for the starved treatment. On a weight-for-weight basis, the two species' daily allocation to reproduction were remarkably similar on starvation, despite *Adalaria* being perhaps up to five times larger. Although *A. proxima* does produce fewer (up to 8) spawn masses than *O. murciata* (up to 19), the greater reliance of *Adalaria* on the earlier spawn masses, in maximizing overall fecundity, is clearly seen from the inclusive and exclusive plots. Resources for these spawnings are accreted over some weeks or months prior to the initiation of spawning. By contrast, the dependence of *Onchidoris* upon recurrent energy intake during the reproductive period is also evident in this figure: clearly, RE values approaching and exceeding 100% (Todd, 1979a; Todd and Havenhand, 1983) can only be supported by such continued feeding. *Adalaria* is, however, considerably less compromised by ration level but, as figures 1 and 2 clearly demonstrate, both reduced and zero energy availability do exert quantifiable contraints on behaviour and fitness. Owing to the patchy and discontinuous distribution of bryozoan prey colonies it is likely that the half-ration regime is not that dissimilar to field circumstances, and such would appear borne-out by figure 4.

Smaller spawn masses for both species comprise fewer embryos/total caloric content than do larger masses (Fig. 5): this is accounted by each egg requiring a minimum (gel) protection and there being a basic caloric cost in constructing a spawn mass. The 'cost per egg' curves decline asymptotically to a size beyond which it becomes no 'cheaper' to package the eggs. Also indicated are the median spawn mass sizes recorded for the summed fully-fed groupings: in each case the nudibranchs are, at least as groups, generally producing the smallest masses which provide the greatest number of larvae per joule invested.

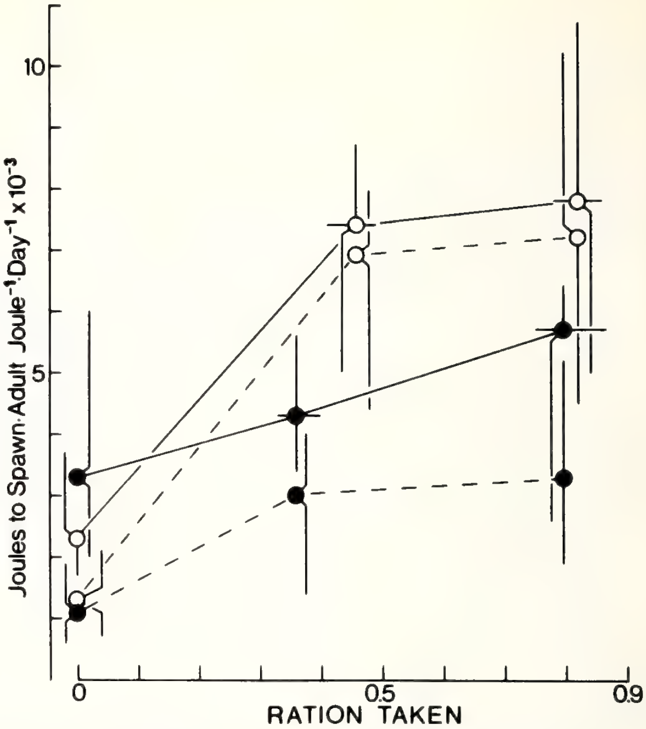

Fig. 4. Daily reproductive "performance" of the two species at varying ration level, scaled for body size and duration of spawning periods. Median values with upper and lower quartiles are shown. Broken plots refer to data from which the first two spawn masses produced by each pair have been excluded.

Consideration of the range of characteristics independently (Figs. 1, 2) shows that, in general, both species responded similarly (on a proportional basis, scaled to the fully-fed controls) to a reduced or zero availability of energy (food) during the reproductive period. Despite the considerable variances distinct patterns of response are apparent. Survivorship, spawn numbers, and spawn sizes all showed, to a greater or lesser extent, decreases with ration level, and intervals between spawnings were particularly increased at zero ration. Perhaps an unexpected outcome was the increase in the proportion of time that the half/zero ration pairs engaged in copulation. Feeding does not, apparently, continue during coupling (pers. obs.). Certainly, for organisms dependent (albeit to differing degrees) upon recurrent energy intake in maximising fitness, such a response was unexpected. Several possible explanations could be advanced, the second of which is presently being experimentally evaluated: 1. Copulation can normally be concluded when the bursa copulatrix is filled, and this can take longer under energetic stress. Certainly, individual oxygen consumption rates decrease markedly upon starvation (unpubl. pers. obs.); 2. Individuals under such stress can catabolize allosperms in the gametolytic gland, and use the products metabolically. The suggestion here is one of individuals attempting to maximize intake by increasing copulatory activity; 3. Energetic stress presumably affects the female function more than the male: the increase in copulation can,

Table 3. Mean egg diameters ±2 standard errors for both species at the three ration levels. n denotes the number of spawn-masses concerned and bars (for *A. proxima* only) indicate significant differences ($P < 0.05$, U-test) between groupings.

	Fully-fed	Half-ration	Starved
Onchidoris muricata	83.0 ± 1.9 μm, n = 18	84.2 ± 1.9 μm, n = 13	84.6 ± 1.5 μm, n = 16
		(No significant differences between groupings)	
Adalaria proxima	167.1 ± 1.4 μm, n = 38	171.6 ± 2.7 μm, n = 10	163.1 ± 1.7 μm, n = 49

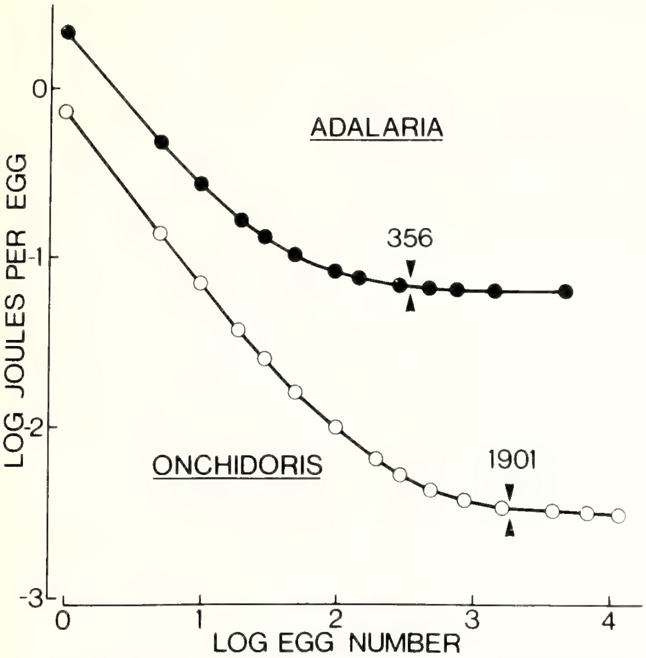

Fig. 5. Relationship between the "cost per egg" in various spawn masses of the range of sizes predicted for each species on the basis of caloric conversions (see Todd, 1979a). The median spawn mass size (control groupings only) for each species is also indicated. See text for further details.

therefore, simply be a response of the individual maximizing its own fitness through its male function.

DISCUSSION

For those organisms which produce more than one clutch or spawn mass during the reproductive period, food availability to the adult is likely to be of crucial importance to not only later offspring production, but also parental survivorship. Most investigations of the effects of ration on reproduction have concerned fish (e.g. Bagenal, 1969; Wootton, 1973, 1977; Reznick, 1983), but data are available for lizards (e.g. Ballinger, 1977), insects (e.g. Collins, 1980; Moeur and Istock, 1980), nematodes (Schiemer *et al.*, 1980) triclads (e.g. Calow and Woollhead, 1977; Woollhead, 1983), and other molluscs (O'Dor and Wells, 1978; Scheerboom, 1978; Russell-Hunter *et al.*, 1984). To date, the only comparable data for a nudibranch concerns Smith and Sebens' (1983) investigation of *Onchidoris aspera* (L.) in New England.

In the case of invertebrates which continue to grow while still reproducing it is apparent that there will be different thresholds of ration necessary to maintain both growth and reproduction (e.g. Scheerboom, 1978). For the present nudibranchs, however, both somatic and total production rates decline during the spawning period [in contrast to, e.g. *Aeolidia papillosa* (L.) (Hall and Todd, 1986)] and, indeed, somatic "degrowth" is invariably observed as soon as spawning commences (unpubl. pers. obs.). Degrowth concerns the decrease in mass of any structural proteins (Russell-Hunter *et al.*, 1984) and is not to be confused with, for example, the inhibition of protein synthesis as a result of reproduction.

The responses of particular organisms to reduced or zero ration varies from one species to another, depending primarily upon the semelparous/iteroparous dichotomy (see, for example, Calow and Woollhead, 1977; Woollhead, 1983). However, Spight and Emlen (1976) noted increases in spawning activity for two (iteroparous) *Thais* species, in response to increase in food supply, while McKillup and Butler (1979) found increases in egg production with decreases in food availability in the similarly iteroparous *Nassarius pauperatus* McKillup and Butler. The British dorid *Onchidoris muricata* is probably closely related to *O. aspera* (studied by Smith and Sebens, 1983) and yet although *O. muricata* displayed reduced reproductive activity under starvation, *O. aspera*, under similar circumstances, failed to spawn at all. Fecundity and body size generally display some form of allometry amongst nudibranch molluscs (Todd, 1979a, b; Todd and Havenhand, 1983; Hall and Todd, 1986). *Adalaria proxima* is small, but up to five times larger than *O. muricata*. Despite the high individual variance in RE for *A. proxima* (see Todd and Havenhand, 1983: Fig. 1), a spawning adult could, on average, produce approximately twice as many equivalent planktotrophic larvae as does *O. muricata*. The question remains: why does it not do so? For *A. proxima* individuals the apportionment of resources toward reproduction is both highly variable and unpredictable. (For *O. muricata* an individual of given size will produce a more-or-less predictable number of offspring.) The suggestion is that the "safer" lecithotrophic strategy reduces the variance and maximises the probability of at least some larval success, but at what selective cost?

The definitive 'per day' evaluation of allocation in relation to ration taken (Fig. 4) demonstrates the overriding interspecific differences. The strategy of *Onchidoris muricata* is to maintain a small body size, degrow slowly (unpubl. obs.) and divert both recurrent energy intake and catabolic products to reproduction. *Adalaria proxima*, by contrast, attains a larger body size, degrows rapidly and seems comparatively incapable (in many individual cases) of exploiting recurrent energy (see Fig. 4). For adult *A. proxima* the situation remains one of unpredictability of allocation between components of individuals' energy budgets (especially respiration, Todd and Havenhand, unpubl. obs.). Selection for lecithotrophy as an adaptive response to this is perhaps only one solution, and one which is probably only open to *A. proxima* because of its absolutely greater reproductive capacity (Todd, 1979a). But this is not to say that reproduction of *A. proxima* is inefficient, ineffective or suboptimal, as figure 5 clearly demonstrates.

I view figure 5 as a clear example of optimised reproductive allocation, for the requisite eggs must be accumulated over a period of days and individuals produce, on average, the most efficient masses with the minimum of delay. Take two extremes: individual A produces very many small spawn masses as soon as the eggs are synthesised, while B accumulates oocytes and produces only a few very large masses. Depending upon the mortality regime to which individual spawn masses are subject it could be that hatching success is maximised for individuals which adopt the strategy of individual B. In reality, however, both individuals would probably perform suboptimally; B may not itself survive to reproduce at all, while A constantly produces "inefficient" spawn mass sizes although maximising its daily productivity.

Much of the available data relating to larval types and reproductive allocation among Nudibranchia have been recently reviewed elsewhere (Todd, 1981, 1983; Hadfield and Switzer-Dunlap, 1984). Of late, interest has focused upon the incidence of extra-zygotic yolk reserves (e.g. Boucher, 1983, 1986; Thompson and Salghetti-Frioli, 1984), in addition to further analyses of metamorphosis of the tropical aeolid *Phestilla sibogae* Bergh (Hadfield, 1977, 1978, 1984; Hadfield and Scheuer, 1985; Kempf and Hadfield, 1985; Miller and Hadfield, 1986; Yool *et al.,* 1986). Reproductive patterns incorporating extra-zygotic yolk appear particularly prevalent among tropical/sub-tropical Ascoglossa (see Clark and Goetzfried, 1978; Clark and Jensen, 1981; Clark *et al.,* 1979), but also feature amongst dorid nudibranchs (Boucher, 1983). Perhaps its most striking consequence is the reduction in cleavage time and embryonic developmental rates conferred by reducing egg size (see Todd and Doyle, 1981).

The utilization of such extra-capsular nutritive reserves I view as being specializations within the usual categories of larval strategies. Notwithstanding this qualification, it is apparent that my convictions of the fundamental importance of the individuals' energetics in playing a part, or perhaps even a major role, in outlining the functional limitations and defining selection for particular larval types, are not shared by Clark and his co-workers (see e.g. Clark and Goetzfried, 1978; Clark *et al.,* 1979; DeFreese and Clark, 1983). Rather, they have invoked the importance of climatic stability and availability/seasonality of (prey) production.

Whatever one's viewpoint, we ultimately require exhaustive investigation of survivorship of both adults and their offspring in the field, rather than just the laboratory. For example, field observations of small, isolated populations of *Onchidoris bilamellata* (L.) showed RE values of only 48 and 63%, in contrast to laboratory values ranging from 114 to 150% (Todd, 1979b). But perhaps more pressing is the need to evaluate specifically the genetic consequences (in terms of larval transport/dispersal potential) of the planktotrophic and lecithotropic strategies. They are clearly not similar means to the same end. Functional energetics could or could not explain why a particular strategy is selectively favoured in certain cases (including the present), but only within a genetic framework will the adaptive significance of these alternatives avail itself of informed judgement. Furthermore, we should be wary of the pitfall of believing in the perfectibility of genotypes. I can only echo the sentiments of Grahame and Branch (1985) in concluding their review of marine invertebrate larval strategies: "...while devising ingenious adaptive explanations for observed features, we must bear in mind that natural selection works with what is available to do only the best necessary job."

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INTERSTITIAL OPISTHOBRANCH GASTROPODS FROM THE WEST EUROPEAN COASTS: REMARKS ABOUT TERATOLOGICAL SPECIMENS

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ABSTRACT

Numerous large dredge and grab samples of sand obtained between 1970 and 1983 from sublittoral sandy bottoms along west European shores (Irish Sea, North Sea, Skagerrak and Western Mediterranean) made possible the collection of 15 species of interstitial opisthobranch gastropods. Among this material only two species were detected with evident abnormal features: *Embletonia pulchra* Alder and Hancock and *Hedylopsis spiculifera* (Kowalevsky). In *E. pulchra* these abnormalities involved rhinophores (lacking or of reduced size); oral veil (absent or of abnormal shape); cerata (either absent, or of abnormal shape or arrangement); rear part of the foot (slender with regard to axis of the body); and body size (reduced with regard to number of cerata). In *H. spiculifera*, abnormal dorsal tegumental verrucosities were present on the visceral hump. These abnormal features are apparently not lethal but are chronic and very rare (< 1/1000). Therefore, they can hardly be linked to any alteration of the natural medium (pollution of the sublittoral sands and gravels where these interstitial opisthobranchs live). They can rather be related to an accidental injury inflicted upon individuals during their larval stages or during their growth, and subsequently imperfectly or not readjusted.

Teratological specimens are common among the molluscs, but their interpretation remains difficult and certainly only a few of them have been detected as abnormal. Fischer (1970) described an aberrant pulmonate gastropod, *Cryptomphalus (Helix) aspera* (Müller), with an abnormal shell, from southern California. A sinistral aberrant of the same species was reported by Basinger (1931). Among the prosobranch gastropods, Sykes (1903) described a monstrosity of *Rissoa parva* Da Costa, in which the later whorls of the shell were smooth, while Gaudio (1985) recorded an anomalous individual of *Astrea rugosa* (Linné) with abnormally sculptured shell. In the cephalopod molluscs, another abnormality is recorded by Smith (1903) in a specimen of *Argonauta argo* L. with thickened shell columella. Among the benthic opisthobranchs, Tardy (1970) observed a great number of teratological individuals of *Aeolidiella alderi* (Cocks) (absence of cerata at rear part of the body) in the aquarium, supplemented by other similar abnormalities recorded from the natural habitat, in *A. sanguinea* (Norman). To date, no such abnormalities have been recorded among the interstitial opisthobranchs. However, during a survey along the West-European shores, collection of numerous individuals of various interstitial opisthobranch species (Poizat, 1978) made it possible to record several forms of abnormalities.

METHODS

A simple but efficient extraction procedure (see Poizat, 1975) made it possible to treat large volumes of sublittoral sediments, dredged or grabbed along West-European coasts: Northern Ireland (Poizat, 1979); Sweden, Bohüslan shores (Poizat, 1980); Yorkshire, U. K. (Poizat, 1981); and Western Mediterranean, France (Poizat, 1978). Subsequently several thousands of interstitial opisthobranchs belonging to 15 species were recovered (Poizat, 1985).

RESULTS

Only two species exhibited abnormalities: *Embletonia pulchra* Alder and Hancock, 1844 (Nudibranchia, Tergipedidae) with serious and numerous abnormal features, resulting sometimes in aberrant specimens; *Hedylopsis spiculifera* (Kowalevsky) (Acochlidiacea) with very few abnormal features. Examples of two additional species, *Pontohedyle milaschewitschii* (Kowalevsky) and *Unela glandulifera* (Kowalevsky), had transient abnormalities restricted to juvenile specimens. Different parts of the body (i.e. rhinophores, oral veil, cerata, visceral hump, foot) were more or less affected by various abnormalities (i.e. absence,

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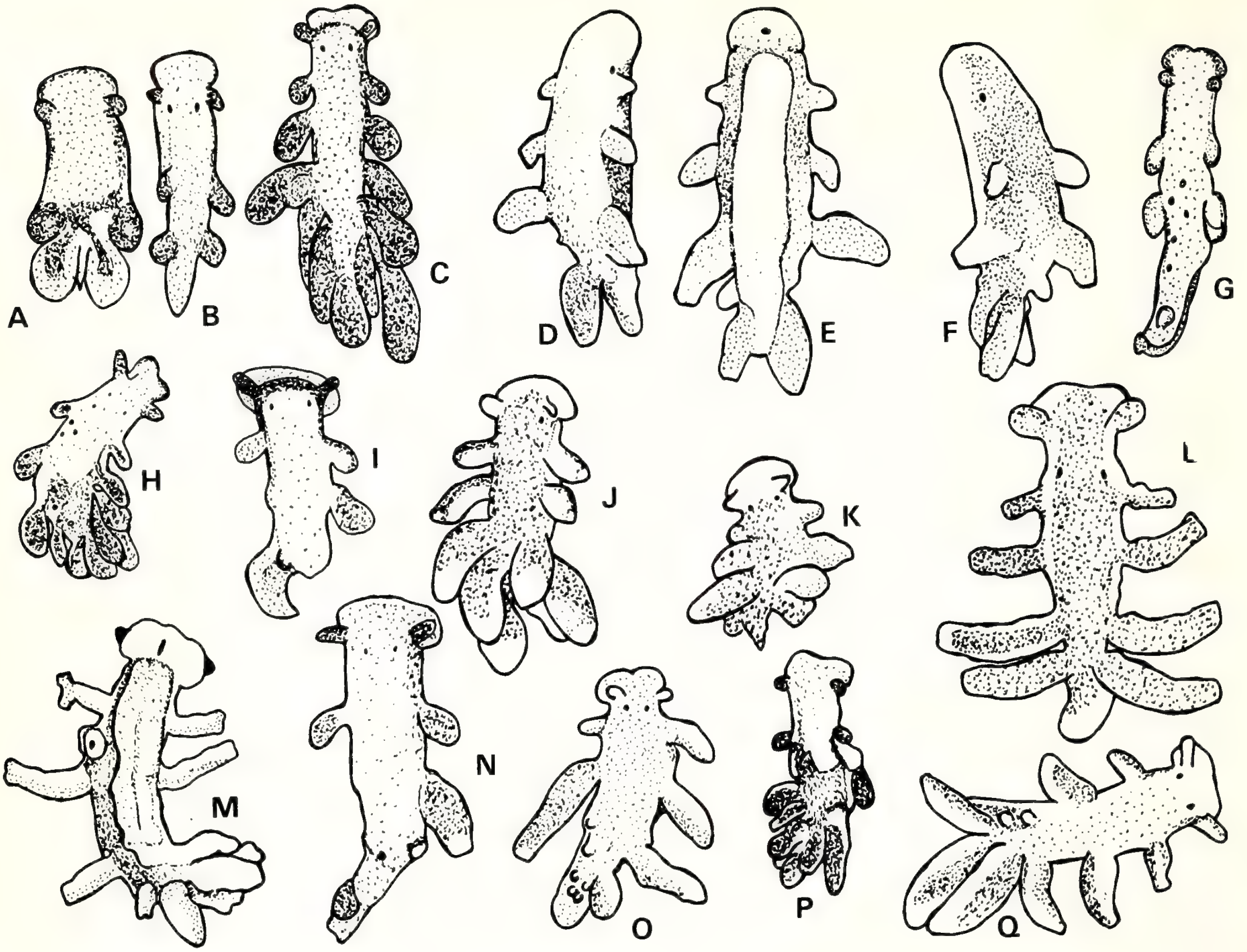

Fig. 1. *Embletonia pulchra* (after photos of living or preserved specimens). **A.** Dorsal view of a juvenile normal living specimen from Western Sweden, 0.4 mm long, with two pairs of cerata, round oral veil, short cylindrical rhinophores. **B.** Dorsal view of a juvenile normal specimen from Western Sweden, 0.8 mm long. **C.** Dorsal view of an adult normal specimen from Western Sweden, 3.0 mm long, with long cylindrical rhinophores, bilobed oral veil and 13 cerata. **D-F.** Right, ventral and left view of an abnormal 1.75 mm specimen from Marseilles, without rhinophores, without oral veil and only five cerata on the right side, four on the left side of the dorsum. **G.** Dorsal view of an abnormal 1.5 mm long adult specimen, from Northern Ireland, with only two pairs of cerata and one odd bud of cerata on the tail. **H.** Dorsal view of a 2 mm long specimen from Sweden, with oral veil of abnormal shape. **I.** Dorsal view of an abnormal 0.6 mm specimen from Northern Ireland, with slender tail. **J.** Dorsal view of an abnormal 1.8 mm specimen from Marseilles, with round oral veil and inflated cerata. **K.** Dorsal view of a small abnormal specimen (1 mm) from Marseilles, with round oral veil and cerata very close to each other. **L.** Dorsal view of an abnormal 1.6 mm specimen from Marseilles, with abnormal arrangement of cerata. **M.** Ventral view of an abnormal 1.6 mm specimen from Marseilles, with bifurcate cerata (genital opening visible between the two first right cerata). **N.** Dorsal view of an abnormal 1.5 mm specimen from Northern Ireland, with round oral veil, low number of cerata and slender tail. **O.** Dorsal view of a 1.6 mm abnormal specimen from Marseilles with buds of cerata on left rear side of the body. **P.** Dorsal view of a 1.7 mm specimen from Sweden, with abnormal arrangement of cerata. **Q.** Dorsal view of an abnormal 1.5 mm specimen from Marseilles, with very long inflated cerata on the right side of the dorsum, buds of cerata on the left side.

aberrant shape, reduced size, etc.) (Table 1). Sometimes two and up to three of these abnormalities coexisted on the same individual, resulting in a very aberrant animal that, however, apparently maintained normal activity patterns.

Embletonia pulchra (Fig. 1). Based on about 1300 European specimens examined, this species appeared most subject to abnormalities. Up to three aberrant features can coexist on the same specimen (Fig. 1K): abnormal round shape of oral veil on adult individual (instead of bilobed), reduced body length and correlatively, cerata very close to each other. Comparing juvenile (body length < 1.5 mm) and adult individuals (Fig. 1A-C) suggests that a round oral veil and small body size and low number of cerata are juvenile features, while conversely, high number of cerata (up to seven on each side

Table 1. Teratological features observed in interstitial opisthobranchs.

Character	Abnormality	Species	Locality	Figures
Rhinophores	1. Lacking (one or both)	*Embletonia pulchra*	Marseilles	1D, F
	2. Reduced size (one or both)	*E. pulchra*	Marseilles	
Oral veil	3. Lacking	*E. pulchra*	Marseilles, Sweden	1D-F
	4. Abnormal shape (round instead of bilobed)	*E. pulchra*	Marseilles	1I, K
Cerata	5. Lacking	*E. pulchra*	Northern Ireland	1G, I
	6. Abnormal shape (bifurcate or inflated)	*E. pulchra*	Marseilles	1M
	7. Abnormal arrangement (asymetric or very close to each other)	*E. pulchra*	Sweden	1P
	8. Abnormal reduced size (buds)	*E. pulchra*	Marseilles	1O, Q
Foot	9. Slender axis of rear part	*E. pulchra*	Northern Ireland	1I, N
Body size	10. Abnormally reduced	*E. pulchra*	Marseilles	1K
	11. Visceral hump reduced in juvenile only	*Pontohedyle milaschewitschii* *Unela glandulifera* *Hedylopsis spiculifera*	Marseilles	
Tegument	12. Abnormal verrucosities on visceral	*H. spiculifera*	Marseilles	2B, C

of the body) correlate with long body size, and bilobed oral veil as adult. Coexistence of some of these juvenile and adult features on the same individual results in a monstrosity (Fig. 1K). Complete lack of oral veil and of rhinophores together with a reduced number of cerata in spite of normal adult size (Fig. 1D-F) has been recorded on the same individual, but this kind of abnormality was rare (< 1/1000). Bifurcate shape of cerata (Fig. 1M) is also a rare aberrant feature. More frequent is the low number of cerata with regard to the body size (Fig. 1G), coexisting sometimes with a slender axis of the rear part of the foot (Fig. 1I, N). Very asymmetric disposition of cerata (Fig. 1G, O-Q) is not uncommon. Still more frequent (> 6/1000) are individuals exhibiting buds of cerata (juvenile features ?) on both or either side of the body (Fig. 1O, Q) in spite of a normal adult body size (> 1.5 mm). For example, a 2.8 mm specimen of *E. pulchra* had seven buds on the left part of the body and seven normal cerata on the right; another specimen (1.62 mm) had five buds of cerata on both sides of the dorsum. Round oral veil (instead of bilobed in normal adult specimens) is found in up to 8/1000 of the European specimens examined and it is frequently associated with atrophy or lack of either or both rhinophores.

Hedylopsis spiculifera (Fig. 2). Among the approximately 2500 individuals collected along the European shores (Fig. 2A), only three specimens from the Gulf of Marseilles can be considered as slightly aberrant: a 1.08 mm (Fig. 2B) and a 1.86 mm individual exhibited one curious verrucosity protruding ahead at both dorsal front sides of the visceral hump. Another individual (1.30 mm) possessed three medio-dorsal verrucosities protruding on its visceral hump (Fig. 2C).

Pontohedyle milaschewitschii and *Unela glandulifera*. Out of approximately 1500 individuals of *P. milaschwitschii* examined and measured in a relaxed fixed state, five very slightly abnormal juvenile specimens (body size < 1.5 mm) were detected by their relatively reduced visceral hump. In normal fixed juvenile specimens, the visceral hump generally corresponds to about 63% of the total length of the animal, while in fixed adult specimens, it corresponds to about 77%. In the most abnormal juvenile specimens collected in the Gulf of Marseilles, with a 0.68 mm body length, the visceral hump (0.30 mm) corresponded to only 44% of the total length. Since such a shortened visceral hump has not been recorded in adult specimens, it must be interpreted as a temporary abnormality that would subsequently readjust during growth. Similar temporary and more unusual abnormalities were observed with *Unela glandulifera* and also with *Hedylopsis spiculifera* corresponding to a very slight temporary negative allometry.

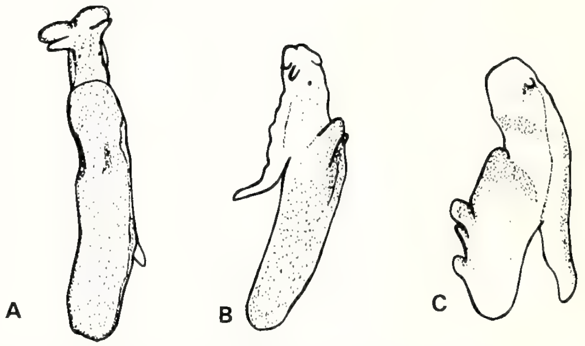

Fig. 2. *Hedylopsis spiculifera* (after photos of living and preserved specimens). **A.** Dorsal view of a normal 1.5 mm adult specimen from Marseilles. **B.** Left view of a 1.8 mm long abnormal specimen with two symetrical expansions at the front dorsal part of the visceral hump. **C.** Right side of a 1.3 mm long abnormal specimen with three odd verrucosities on the doral median line of the visceral hump.

DISCUSSION

The teratological features described here are extremely unusual and therefore cannot be related to pollution. They are not lethal since the aberrant animals remained normally active several days after they were collected and had the same behaviour as normal ones, apart from the fact that no reproductive activity was exhibited by normal nor abnormal specimens. In Tardy's (1970) observations the teratological features recorded for *Aeolidiella alderi* were also not lethal, the more so as the adults descending from aberrant parents were normal and able to reproduce.

Most of the teratological features recorded on interstitial opisthobranchs in their natural habitat are probably chronic, especially because they proved to concern mainly adult specimens, the growth of which has stopped and therefore without possibility of correction. However, two categories of abnormalities can be distinguished and explained differently: the lack of one or several body parts; malformations of existing structures. For example, total lack of oral veil and/or rhinophores in *Embletonia pulchra*, and also total or partial lack of cerata on adults can be due to a serious and early perturbation during larval life definitely interrupting the normal development of the injured parts of the embryos. Precisely, Tardy (1970) interprets the teratological specimens of *Aeolidiella alderi* as resulting from such an accidental perturbation during early larval stages. On the contrary, malformations such as slender axis of the tail, buds of cerata or rhinophores, bifurcate cerata on adult *Embletonia pulchra* and verrucosities on the visceral hump of *Hedylopsis spiculifera,* probably result from a slight injury inflicted upon the individuals after their larval period, during their growth at a time when readjustment is still possible. This regeneration however can occur in an abnormal way. The monstrosity recorded by Sykes (1903) in *Rissoa parva* probably results from such a slight injury to the animal during its post larval growth, leading to an aberrant readjustment.

In general, it appears that either abnormal or normal regeneration remains possible provided the injury is not too serious. For example, in Tardy's experiments (1970) the removed cerata regenerate (on adult specimens) only if the gut diverticulum has not been excised. Other experiments (see Poizat, 1971; Poizat *et al.*, 1981) concerning adult specimens of interstitial opisthobranchs, such as microsurgical removal of the rhinopores of *Hedylopsis spiculifera*, or chemical treatment with mercuric chloride of *Pontohedyle milaschewitschii* lead to the same conclusions. In *P. milaschewitschii,* regeneration of the oral veil remained possible only if the concentration of mercuric chloride does not exceed 0.08 g/*l* sea water during 20 hr (sublethal dose) and if the animals were returned to normal sea water. In such condition, the tegument of the animals that represents their respiratory organ had not been deeply injured and therefore, readjustment was normal and complete. Microsurgical removal of the rhinophores of adult *H. spiculifera* was also followed by a total and normal regeneration in about 26 days (Poizat, 1971), because the excision was restricted to a very small area where morphallaxis phenomena seemed to occur.

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